

COMPETITION BETWEEN YOUNG-OF-THE-YEAR
NORTHERN PIKE (Esox lucius) AND WALLEYE (Stizostedion vitreum)
UNDER NATURAL AND EXPERIMENTAL CONDITIONS

BY
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A Thesis submitted to
The Faculty of Graduate Studies
In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Department of Zoology
University of Manitoba
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ABSTRACT

Competition between young-of-the-year (YOY) northern pike (Esox lucius) and walleye (Stizostedion vitreum) was investigated under natural and experimental conditions. Summer habitat and food use of YOY pike and walleye in Whitefish Lake, Manitoba were compared. Habitat overlap was greatest in the early summer; there was also considerable overlap in prey type and size throughout the summer, despite the fact that pike were significantly larger than walleye. These similarities indicated a potential for competition. The hypothesis that YOY pike and walleye compete when food-limited was directly tested by manipulating fish density and prey availability in enclosures under semi-natural conditions. Intraspecific competition was demonstrated for both species in three of four trials. Interspecific competition was detected in the two trials with the smallest fish and favoured pike. Pike had significant negative effects on the production and prey consumption by walleye in these trials. Possible mechanisms by which pike may have outcompeted walleye for prey are discussed. In later trials intraspecific and interspecific competition were equal in their effects on production and diet, or were not detected. Foraging efficiency can influence competitive dominance, so a laboratory experiment was used to test the hypothesis that relative feeding success of YOY pike and walleye changes under different conditions of light level and turbidity. Walleye feeding success was lower with each trial in clear compared to turbid water, and always higher than that of pike in turbid water. Few differences were detected for pike in clear versus turbid water; this was unexpected and possible reasons for this outcome are given. My conclusions are that in clear lakes, competition is most likely to occur in the early summer before YOY pike and walleye separate in habitat and temporal activity patterns. Pike are expected to outcompete walleye under these conditions. In a turbid environment, reduced spatial and temporal segregation throughout the summer may prolong the potential for competition. Walleye could be the dominant species in turbid environments because of their superior foraging ability. Competition may influence year-class strengths directly and also indirectly by predisposing poor competitors to predation or harsh environmental conditions.

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GENERAL INTRODUCTION

GENERAL INTRODUCTION

In this thesis I examine the nature and degree of competitive interactions among young-of-the-year (YOY) northern pike (Esox lucius L.) and walleye (Stizostedion vitreum Mitchill). I use samples from natural populations (Chapter I), an enclosure experiment (Chapter II), and a laboratory experiment (Chapter III) to do this.

Northern pike and walleye are of ecological importance in freshwater fish communities because they are the top predators in many temperate coolwater systems. They also have considerable economic importance for commercial and sport fisheries throughout their geographical range. An understanding of the factors affecting the growth and survival of pike and walleye is therefore important to both fisheries ecology and management. The year-class strength of both species fluctuates annually and is thought to be determined usually by the end of the first summer (Hunt and Carbine 1951; Franklin and Smith 1963; Forney 1966; 1976; Serns 1982a; Craig and Kipling 1983). Predation and starvation mortality are strongly linked to the body size of small fish (Werner 1986; Post and Evans 1989a; 1989b), so there should be selective pressure for YOY to grow at a maximum rate. Competition among YOY fish is one process which may influence year-class strength, through its effect on growth and survival.

In addition to its potential effect on year-class abundance, there are several other reasons why competition might be more important for YOY than for older fish. Resource limitation is a necessary prerequisite for competition to occur (Birch 1957), and the growth and survival of

smaller fish is more sensitive than the growth of adults to the stress of a limited food supply (Colby et al. 1987; Post and Evans 1989b). Furthermore, YOY fish cannot utilize as large a size range of prey as adults (MacLean and Magnuson 1977) so food limitation may affect younger size classes more frequently. The potential for competition also may be strongest because of a greater overlap in habitat and diet between YOY pike and walleye than between adults; the degree of this similarity will be investigated in this thesis. Lastly, individuals of most fish species vary greatly in size and many undergo marked morphological and physiological changes as they grow. These changes complicate species interactions because different size classes of individuals influence others in varied and sometimes opposite ways (Werner 1986). For example, top predator species are often zooplanktivores as larvae, but their piscivorous feeding morphology may make them poor competitors with the smaller zooplanktivorous fish species which later become their major prey. The complexity of interactions in size structured fish communities makes the detection and evaluation of competitive effects at the population level a challenging and difficult task. Given the foregoing, I felt that it would be most profitable to investigate competition among YOY fish.

There has been considerable controversy in recent years over the importance of competition in the structuring of natural communities (Wiens 1977; Connell 1980; Schoener 1982; Connell 1983; Sih et al. 1985; Roughgarden and Diamond 1986). The controversy centres around whether competition is the major ecological interaction influencing natural selection, or is in fact only intermittent in effect due to overriding

influences on population density such as predation and the abiotic environment. A great variety of observational work has been published detailing resource utilization and niche partitioning among similar species, as well as theoretical developments of the well known mathematical models of competition by Lotka (1932) and Volterra (1931) (eg. reviews by Schoener 1974; Pianka 1976). Until the early 1970's, most findings were interpreted as being in support of current competition theory. At that time, the importance of competition was widely accepted and its influence on population dynamics and community structure strongly advocated. A number of criticisms of the theory arose by the mid-1970's however, challenging the way in which competition had been studied and understood (eg. Connell 1975; Peters 1976; Menge and Sutherland 1976; Wiens 1977).

A primary criticism was the way in which niche overlap measures had been used to demonstrate competition, interspecific competition in freshwater communities being no exception. Ross (1986) reviewed over 230 studies of resource use and concluded that there was substantial partitioning of food and habitat as well as temporal separation among co-occurring fish species. The suggestion often made that northern pike and walleye compete has also largely been based on evidence of overlap in diet (eg. Scott and Crossman 1973; Anthony and Jorgensen 1977; Forney 1977; Swenson and Smith 1976; Colby et al. 1987). But the important prerequisite that the shared resource be in limited supply was not assessed in many studies of niche overlap, and the relationship between the degree of overlap and the intensity of competition is far from clear. Classical competition theory predicts that greater overlap

results in more intense competition, but observational data and field experiments have sometimes demonstrated the opposite (Schoener 1983). Furthermore, fish species may differ in resource use for reasons other than avoidance of competition, and utilization traits often vary greatly both seasonally and between different life stages.

It seems clear that competition and resource overlap are not always related. More importantly, it is apparent from the above criticisms that overlap should not be used to detect or measure the intensity of competition, but only to infer that there is a potential for it to occur. This is the aim of the first section of my research. Although a considerable literature on the early life histories of pike and walleye is available, I am unaware of any studies which sample YOY pike and walleye concurrently in order to directly compare their habitat and food use. I undertook this objective by collecting fish samples in Whitefish Lake, Manitoba, where naturally reproducing populations of pike and walleye occur together. The results are presented in Chapter I. An assessment of the potential for competition between the two species serves as a logical introduction to the other two chapters, in which I examine the nature and degree of competitive interactions under experimental conditions.

Other indirect methods besides niche overlap studies have been used to investigate competition among freshwater fish species. One method has been to examine differences in patterns of resource use between species in sympatry and allopatry. The detection of a niche shift by one species in sympatry with another species, compared to when they are allopatric, constitutes indirect evidence for interspecific

competition. Some of the best examples are from communities of relatively low complexity, such as the lakes containing salmon and charr populations in Scandinavia (Nilsson 1963; 1965; Svärdsön 1976), and North America (Andrusak and Northcote 1971; Nilsson and Northcote 1981; Hindar et al. 1988). These communities are species-poor, making it easier to infer competition from niche shifts demonstrated by one species when in the presence of another (Werner 1986). In contrast, northern pike and walleye belong to the typically more species-rich mesothermic freshwater community, in which community organization and hence interspecific interactions are often of greater complexity. Direct comparisons of their resource utilization traits in sympatry and allopatry have not been made, perhaps because of this complexity. Johnson et al. (1977) compared the limnological characteristics of Ontario lakes containing each of these species alone and together. They suggested that the high number of small lakes containing only pike may be due to a low probability for walleye to successfully coexist with pike. Small lakes often do not provide open-water habitat for walleye, which may be required for niche separation between the species when in sympatry.

Evidence for competition has also been derived from long-term studies of changes in relative density, growth, or resource use following species introductions, removals or other changes in abundance. Forney (1977) concluded that an increase in walleye recruitment was caused by reduced interspecific competition following a decline in pike density in Oneida Lake, New York. Increased intraspecific competition for limited prey was suspected to have prevented a concurrent increase

in walleye growth rates. In contrast, removals of adult walleye over a 6 year period in two experimental lakes in north-central Ontario had no obvious influence on pike abundance (Colby et al. 1987). Similarly, no relationship was found between adult walleye and pike abundances made over an 11 year period in Escanaba Lake, Wisconsin (Colby et al. 1987). Colby et al. (1987) infer from these latter examples that competition may not be of significance to adult walleye and pike, although the findings in Oneida Lake contradict this conclusion.

Other manipulations, involving the stocking of YOY pike and walleye, showed more consistent evidence of competition. In Grace Lake, Minnesota, fry and fingerling pike were stocked successfully over an 8 year period in the 1950's (Wesloh and Olson 1962). Walleye abundance briefly increased before decreasing by the mid 1970's to 20 % of peak numbers. An improved walleye sport fishery following the pike introduction was attributed to increased vulnerability to angling caused by competition between walleye and pike for prey (Wesloh and Olson 1962). Pike fingerlings were also successfully stocked into Horseshoe Lake, Minnesota, in 1969, 1973, and 1979. Numbers of walleye declined during this period, despite repeated stocking of walleye fingerlings; there was also a decline in second year growth of walleye. Harriet Lake, Minnesota, had an abundant pike population until a removal operation commenced in 1974 as part of a decision to manage the lake for muskellunge (Esox masquinongy). Attempts at stocking walleye before this time had failed, which is consistent with the suggestion that juvenile walleye cannot coexist with pike in small lakes. After the removal of

pike, introductions of walleye resulted in a large walleye population of fast growing individuals (Colby et al. 1987).

I think that these long-term 'natural experiments' indicate that competitive interactions can influence pike and walleye growth and abundance, although certainly not in all systems. They also provide evidence that smaller fish may be more likely to compete than adults. Manipulations such as these lack controls however, and the results are often only qualitative in nature. As such, they are subject to the criticism that other uncontrolled factors, such as predation by adult fish, are responsible for the observed patterns.

The most direct way to detect competition is by use of controlled field experiments designed to separate and compare the effects of intraspecific and interspecific competition (Schoener 1982; Connell 1983; Diamond 1986; Fausch 1988). Field experiments have been conducted with a few freshwater fish species (eg. Werner and Hall 1977; 1979; Clady and Luker 1982; Hanson and Leggett 1985; 1986; Persson 1987a; 1987b), but many of these suffer from a combination of incomplete design, a lack of proper replication, or unnatural experimental conditions. However, they do detect competition in freshwater fish communities in a far more convincing manner than is possible with the other types of evidence already described. Competition between northern pike and walleye has not been investigated by any type of field experimentation. Chapter II of this thesis presents the first such experiment testing the hypothesis that YOY walleye and pike compete when food-limited. The experiment was designed to detect and compare the intensity

of intraspecific and interspecific competition by manipulating fish density in enclosures.

Field experiments are extremely useful for the examination of population responses to some treatment effect (eg. a change in abundance), but they rarely examine the mechanism behind the observed effects (Schoener 1983; Diamond 1986). For example, the behavioural or physiological differences that may enable pike or walleye to outcompete the other for prey cannot be ascertained by a field experiment alone. Supplementary data or information are required to investigate these mechanisms. I conducted laboratory experiments on the foraging ability of YOY pike and walleye with this objective in mind. The experiment presented in Chapter III tests the hypothesis that different visual conditions created by different levels of turbidity and light intensity can affect competitive ability through an effect on foraging success. The assumption is that competitive dominance is dependent on the environmental conditions which influence the mechanisms underlying competitive interactions.

A more comprehensive understanding of ecological processes such as competition can be achieved by combining methodologies that each yield information not available from the others (Diamond 1986). In this thesis the different methods used in each chapter complement one another in this manner. A general discussion following these chapters integrates the information and conclusions derived from each investigation.

Chapter I:
Habitat, food, and growth of young-of-the-year
northern pike and walleye in a Manitoba lake

INTRODUCTION

Evidence of niche overlap has been used in the past to determine the presence and importance of competitive interactions among similar freshwater fish species (Hunt and Carbine 1951; Keast 1965; Swenson and Smith 1976; Crowder et al. 1981; Schmitt and Coyer 1983; Tonn and Paszkowski 1987). This type of study has come under criticism because the relationship between competition and overlap in resource use is unclear (Holt 1987). Species may be similar in their utilization of some resources, but very different in their use of others. Overlap may vary seasonally or between different life stages (Wiens 1977; Grant 1986; Werner 1986). Species also differ in their use of a resource for reasons other than competition. For example, habitat choice can reflect responses to structural features such as vegetation, to physical factors such as temperature gradients, or to biotic influences such as the distribution of predators, or food, or competitors. The intensity of competition also can not be judged by an examination of resource utilization traits alone (Schoener 1982). Competition will not be important if the shared resource is in plentiful supply, or if predation or other factors reduce the population density of potential competitors to levels at which interactions do not occur (Connell 1975; Wiens 1977; Sih et al. 1985). Low overlap may indicate that competition is in fact important, for example if species partition habitats because natural selection favours individuals that avoid interspecific competition (Holt 1987).

It is apparent that there are many problems with inferring exploitative competition from niche overlap. Despite this, it is important to note that individuals must utilize a common resource for competition to occur, and therefore that evidence of overlap in resource use is still an important prerequisite for a more direct examination of competition.

There are many axes along which niche overlap can be measured. Reviews of resource partitioning among freshwater fish species indicate that the most important of these are habitat, food, and temporal segregation (eg. Ross 1986). Northern pike and walleye have often been cited as competitors based on evidence of dietary similarities (Scott and Crossman 1973; Anthony and Jorgensen 1977; Forney 1977; Swenson and Smith 1976; Craig and Smiley 1986; Colby et al. 1987). Adult pike and walleye differ in their habitat use in many lakes however (Ryder and Kerr 1978). Pike prefer inshore, weedy habitats (Diana 1980; Chapman and Mackay 1984), whereas walleye are demersal predators and tend to be more offshore (Scott and Crossman 1973; Ryder 1977). This difference is partly due to the walleye's tapetum lucidum which adapts it to habitats of low light availability (Moore 1944; Ryder 1977). Adult pike and walleye also differ in daily feeding periodicity, because of the difference in the light intensity that each requires for optimal prey capture. Overlap in food use between adult fish could therefore be reduced because of habitat and temporal segregation.

Competition between young-of-the-year (YOY) fish may be an important influence on their growth and hence survival, because body size and mortality are strongly linked (Werner 1986; Post and Evans 1989a, 1989b). Colby et al. (1987) suggested that interactions between

species are most likely to influence abundance when they occur during early life stages. Thus competition among YOY pike and walleye could have an important influence on cohort strength but this has not been directly examined. Although evidence from the literature indicates that similarities in pike and walleye resource use may be strongest during their first summer, direct comparisons have not been made.

YOY walleye are initially pelagic zooplanktivores until they are approximately 20-25 mm in total length (Houde and Forney 1970; Bulkley et al. 1976). They then become demersal and prey on benthic invertebrates and later on small fish, if available. Piscivory has been noted in walleye as small as 20 mm (Bulkley et al. 1976). YOY walleye are found inshore in the shallow littoral zone during this period of transition but move offshore late in the summer (Forney 1966; Johnson 1969; Johnson et al. 1988). YOY pike undergo the same changes in prey choice at the same sizes (Hunt and Carbine 1951; Frost 1954). Unlike walleye, they remain inshore, preferring shallow weedy areas as YOY, juveniles, and adults (Hunt and Carbine 1951; Franklin and Smith 1963; Diana 1980; Chapman and Mackay 1984).

Thus it appears that there is strong potential for pike and walleye to overlap in diet and habitat during their first summer. The studies described above were separate investigations of the early life histories of each species however. I am unaware of any studies which directly compare resource use by YOY in a lake containing both pike and walleye. Therefore the purpose of this component of my research was to examine niche overlap between YOY pike and walleye by comparing their habitat and food use, both temporally and spatially, in the natural

environment. Changes in patterns of resource use with both species' growth and development were examined. By doing this, an assessment was made of the potential for competition between pike and walleye throughout their first summer.

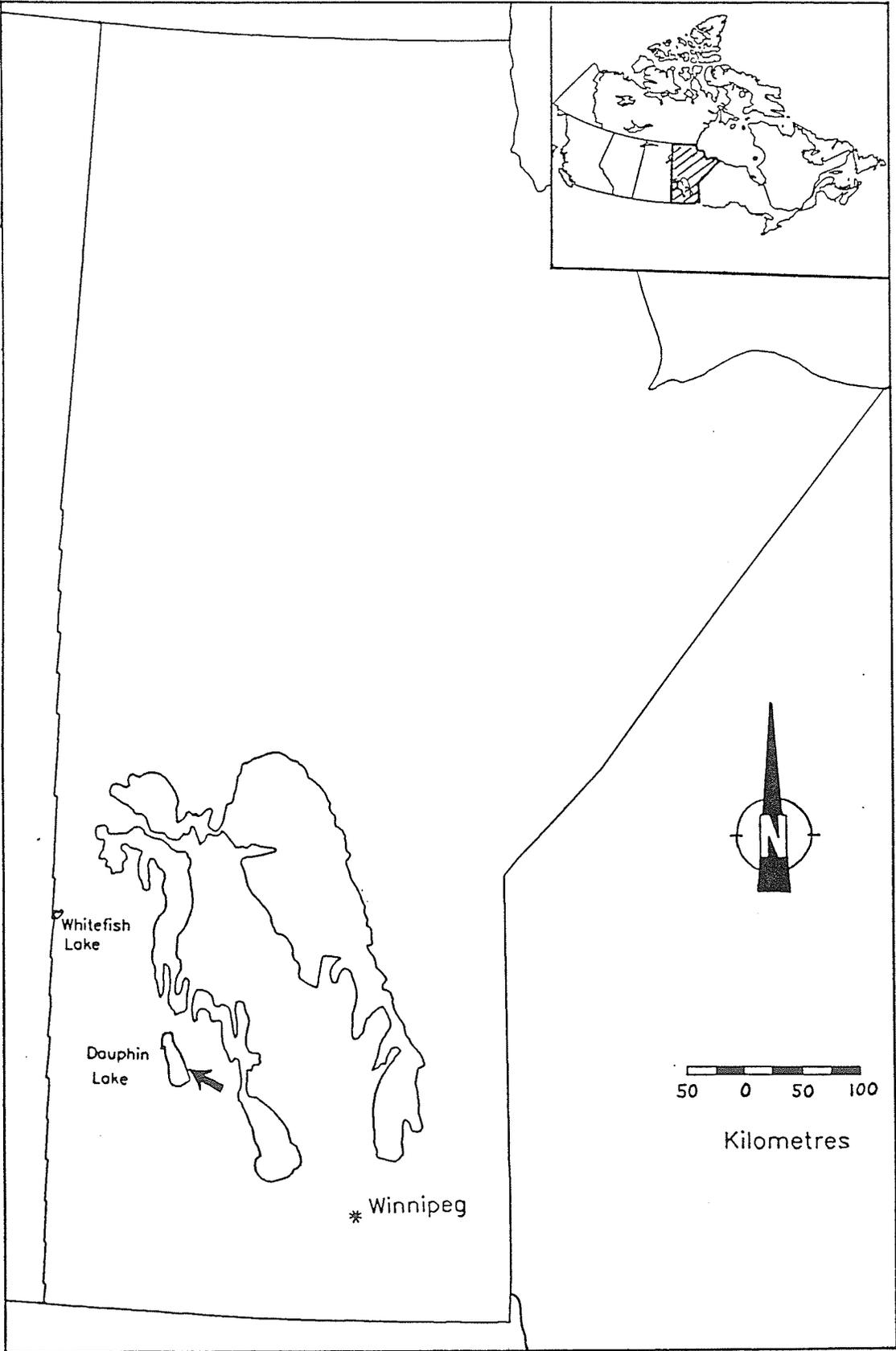
MATERIALS AND METHODS

Study Area

Whitefish Lake, Manitoba (52° 20' N, 101° 36' W), situated in the Porcupine Mountain Provincial Forest, was chosen for study (Fig. 1). Natural populations of northern pike and walleye co-occur in the lake; neither population has been manipulated or enhanced by stocking or other management practices (Hugh Valiant, Manitoba Dept. of Natural Resources, pers. commun.). It can therefore be assumed that any patterns in habitat and food use are a reflection of long-term coexistence and the influence of the local environment.

Whitefish Lake is a 675 ha lake with mean and maximum depths of 8.6 and 19.5 m, respectively. Secchi depth, conductivity, dissolved O₂, and water temperature were measured during each sampling period in this study. Specific methods and a summary of results are provided in Appendix 1. Whitefish Lake is popular amongst anglers; species caught include walleye, pike, yellow perch (Perca flavescens), lake whitefish (Coregonus clupeaformis), cisco (Coregonus artedii), burbot (Lota lota), and white sucker (Catostomus commersoni). Test gillnetting has been conducted infrequently by Manitoba fisheries personnel. The size

Ch. I, Figure 1. Map of Manitoba, showing Whitefish Lake, site of the field study (Chap. I), and Dauphin Lake, site of experimental work (Chaps. II and III). The arrow points to the location of the Department of Fisheries and Oceans Methley Beach Walleye Research and Rehabilitation Station beside Dauphin Lake.



frequency distributions and the presence of large, old pike and walleye in most catches are indicative of lightly exploited populations (unpubl. data). Insufficient data are available to estimate the relative densities of either species. The limnological data and the species composition of the lake indicate that it is typical of coolwater fish communities found in Canadian Shield lakes (Johnson et al. 1977; Ryder and Kerr 1978).

Procedure

Fish were collected on five occasions at three week intervals (except the last) during the summer of 1987. Sampling dates were: June 2-4, June 22-25, July 13-17, August 3-7, and September 22-25. Samples were collected at three times of the day: dawn (starting at sunrise: 05:00-07:00), midday (12:00-15:00), and dusk (19:00-20:30, depending on sunset). Four habitat areas (pelagic (upper water column), littoral (shallow inshore), and shallow and deep offshore zones) that were expected to contain pike and/or walleye were sampled. These were classified according to water depth, since depth is related to other variables of more direct importance to the fish. Prey abundance, provision of cover, and abiotic factors such as temperature and oxygen are probably the most important of these. I sampled the upper pelagic zone for post-larval fish in early June only. The shallow littoral zone (< 2 m depth) was sampled on all occasions. This inshore habitat had the greatest abundance of submersed vegetation. The offshore lake bottom was sampled for demersal fish at two depths on the second and subsequent sampling

periods. The shallower depth was at the outer margin of aquatic plant beds; the deeper zone had a sand-silt substrate devoid of vegetation. Different types of gear were required for each of these areas; a description of each follows.

I used paired bongo nets to sample for pelagic fish in early June. Each net consisted of an aluminum mouth-reducing cone and attached NitexTM netting of 505 μm mesh. The cone mouth opening was 0.25 m in diameter. The nets were 2.7 m in length, decreasing in diameter from 0.50 m at attachment to the cones, to 0.12 m at the rear collection jars. The two bongo nets were joined to an apparatus that attached directly to the bow of a boat. Both nets were fished just below the surface in water 2-5 m deep. Fish were removed from the collection jars immediately after each tow and preserved in 5 % formalin. Catches from the two nets were pooled because they were not independent replicate samples.

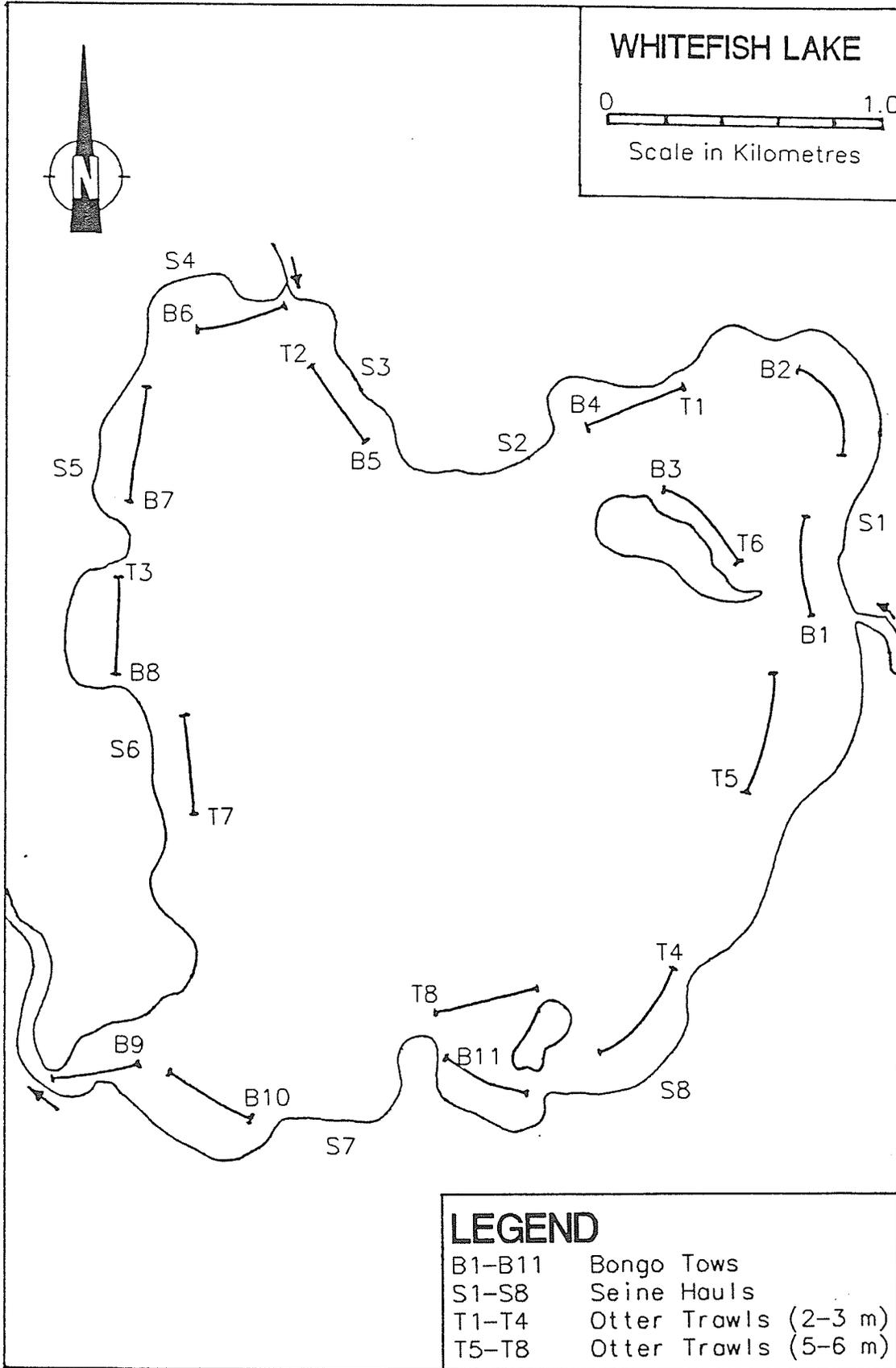
I restricted bongo sample locations to inshore areas because wind-driven currents tend to congregate larval fish near windward shores (Houde and Forney 1970), and because of the difficulty of using the gear offshore. Eleven areas around the lakeshore were found where a 3 minute tow could be made along a relatively straight line over the chosen depth contour (Fig. 2). The plan was to randomly choose six of these locations for sampling during each of the three times of day, and to make two tows at each location. Due to stormy weather however, no midday tows were done, and only three locations were sampled in the evening. Dawn samples were made over two consecutive days (Table 1).

Fish were collected inshore in the shallow littoral zone with an 18.3 m beach seine. Mesh size was 1.6 mm, unstretched, and the seine depth was 2.0 m. Eight sections of shoreline suitable for seining were found (Fig. 2). Each location was a sand or pebble beach. Bays with emergent vegetation and rocky shorelines could not be sampled by seine. Six locations were sampled at dawn, midday, and dusk by randomly choosing three of the eight locations on two consecutive days. A large number of hauls were attempted during the first sampling trips but then reduced to six because of time limitations. As a result, sample sizes are inconsistent for these periods (Table 1).

The seine was set from a boat by deploying it parallel to shore in approximately 2 m of water. Ropes (22 m long) tied to each end of the seine were used to pull it to shore. All fish less than 10 cm total length and all YOY pike and walleye were preserved in 5 % formalin. Larger fish were enumerated and released.

I collected demersal fish along two depth contours (2-3 m and 5-6 m), using an otter trawl. The trawl had a 5.7 m footline and a body of 2.5 m stretched mesh, narrowing to a cod end lined with 0.4 m stretched mesh. Four transects were chosen along each of the depth contours (Fig. 2). Two locations at each depth were drawn for each time period, on two consecutive days. Initially two tows were made at each location, a total of eight samples for each time of day (2 locations x 2 tows x 2 days). I reduced the number to six after the July period to make sample sizes consistent with the seine hauls (Table 1). Each trawl sample consisted of a 3 minute tow at approximately 5.6 km/h, covering

Ch. I, Figure 2. Sample locations on Whitefish Lake, Manitoba ($52^{\circ} 20'$ N, $101^{\circ} 36'$ W). Seine locations are on sand or rubble beaches; bongo tows were just below the water surface, at depths of 2 - 5 m.



Ch. I, Table 1. Number of samples collected in Whitefish Lake with each gear during each time of day, by sample period. Each sample is one bongo tow (nets combined), seine haul, or otter trawl. Missing numbers indicate gears not used at those times.

Date	Time	Bongo	Seine	Otter, Shallow	Otter, Deep
June 2 - 4	dawn	12	6	-	-
	midday	-	12	-	-
	evening	6	6	-	-
June 22 - 25	dawn	-	6	4	4
	midday	-	8	6	10
	evening	-	9	6	7
July 13 - 17	dawn	-	6	8	8
	midday	-	6	8	8
	evening	-	6	8	8
August 3 - 7	dawn	-	6	6	6
	midday	-	6	6	6
	evening	-	6	6	6
Sept. 22 - 25	dawn	-	6	6	6
	midday	-	6	6	6
	evening	-	6	6	6

an estimated distance of 280 m. Fish were collected and preserved using the same criteria described above.

Analyses

The fish in each sample were identified to species and counted. The total weight of all fish in each seine was measured and used to estimate mean littoral fish biomass for comparisons with other lakes (Chap. II). YOY pike and walleye were weighed and their fork lengths measured. I tested for interspecific differences in mean fork length and weight within each sample period using t-tests on transformed data. Taylor's power plot analysis (Elliot 1977) was used for both length and weight data to determine the appropriate transformations to stabilize variance. These were: $(\text{fork length})^{0.3}$, and $\log(\text{weight})$.

Habitat use

Catches of YOY pike and walleye were very low. Only 23 % of all samples ($n = 276$) contained one or both species, and of these, 67 % contained only one fish of either species. This result limited the amount of quantitative comparisons that could be made with these data. Furthermore, it would be inappropriate to compare absolute catches in different areas because of the different numbers of samples taken in each, and more importantly, because of the different selectivities of the various gears. It was for these reasons that I did not use the catch data to estimate fish density or catch per unit effort for comparisons between species.

Instead, comparisons were made between the relative distributions of pike and walleye among the sampled habitat areas. Although catches were undoubtedly biased because of the gear selectivity or the number of samples taken, these influences were assumed to be approximately equal for the two species in any given habitat. Therefore the habitat distribution of the total catch of each species could be compared within each sampling period. This was accomplished by using two-way chi-square contingency tests for differences in probabilities (Conover 1980), wherein rows were the two species and columns were the habitats sampled during each period. The null hypothesis of this test is that the probability of being in each habitat (column) is the same for both populations (rows), or equivalently, that the species ratio is the same in each habitat (Conover 1980). Samples were pooled within each sample period because catches were too small to compare distributions within each time of day. Therefore an analysis of the temporal distribution of pike and walleye was made in a more qualitative manner. I classified each habitat x time of day combination in terms of whether pike and walleye were present or absent. This allowed a simplified evaluation of where fish of each species were caught at each time of day.

Food use

Prey items found in pike and walleye stomach contents were grouped into the following taxonomic categories: Copepoda, daphnids, Amphipoda, insects, other invertebrates, white suckers, spottail shiners (Notropis hudsonius), johnny darters (Etheostoma niger), yellow perch, and fish remains. The total length of each whole invertebrate prey item was

measured with an ocular micrometer mounted in a dissecting microscope. Prey fish were measured with a ruler.

Low sample sizes also prevented an examination of intraspecific and interspecific differences in food use between pike and walleye in dawn, midday, and evening samples, or between fish in the various habitats. I therefore pooled stomach samples from the different habitats and times of day within each sampling period and compared overall patterns in pike and walleye diet composition and prey size over the summer. Stomach contents of individual fish were characterized as the proportion of items (by numbers) in various prey categories. The mean proportions (expressed as %) of individual diets that were of each prey type were then calculated for each sample period. This method was chosen over the common procedure of pooling all individuals before calculating proportions, which constitutes sacrificial pseudoreplication (Hurlbert 1984; Krebs 1989). Prey which are numerically rare but occur in many stomachs are not well represented in estimates of dietary proportions based on numbers, but clearly may be of great importance in a diet (eg. a small number of large items). The frequency of occurrence of each prey type, as a percentage of stomachs, was also used in order that this possibility be addressed.

I compared the mean size of prey items in pike and walleye stomachs within each sample period using Mann-Whitney U-tests, after testing for and finding no within-species differences between habitats and times of day (Kruskal-Wallis tests, $p \gg 0.05$). Non-parametric tests were used because the data were non-normal and heteroscedastic, even when transformed. Prey length frequency distributions were also calcu-

tated for pike and walleye in each sample period to illustrate the degree of overlap in the size range of their prey.

RESULTS

Sixteen species of fish were caught in the three types of gear (Table 2). Northern pike and walleye occurred infrequently in the samples. A total of 70 pike and 47 walleye were collected over the summer. As noted in the Methods section, the majority of the 276 samples (77 %) contained neither species. Of 64 samples with pike and/or walleye, 43 of these had only one individual. The greatest numbers were collected in the first two sampling periods. A subsequent decline in catches probably reflects increased net avoidance with increasing size, or declining abundance, since sampling effort within each habitat was approximately equal over the summer (Table 1).

Northern pike were significantly larger in fork length than walleye in each month of sampling (Table 3). The ranges in fork length for each species overlapped in August and September however. Differences in weight were not significant in these latter two sampling periods, but highly significant in June and July samples (Table 3). The lack of a significant weight difference in September is due at least in part to low sample size. However a plot of mean sizes illustrates that pike growth slowed between July and August (Fig. 3) Furthermore, individual fork lengths and weights of the two species do not overlap until August and September. These findings indicate that size differences between pike and walleye were not as pronounced in the older YOY.

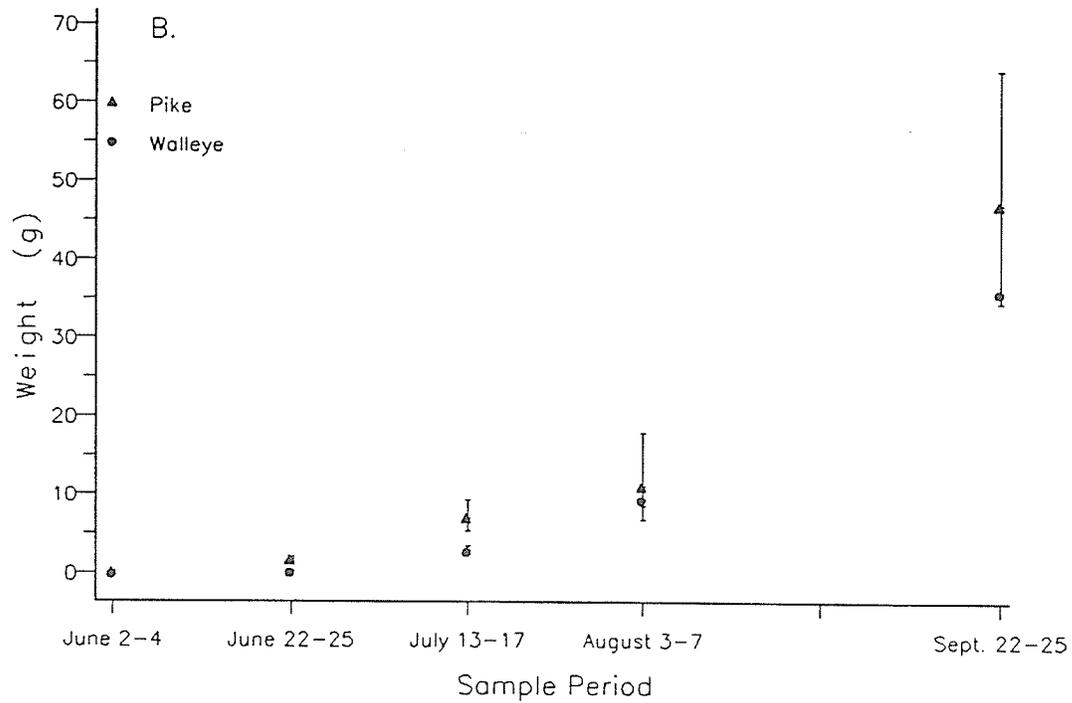
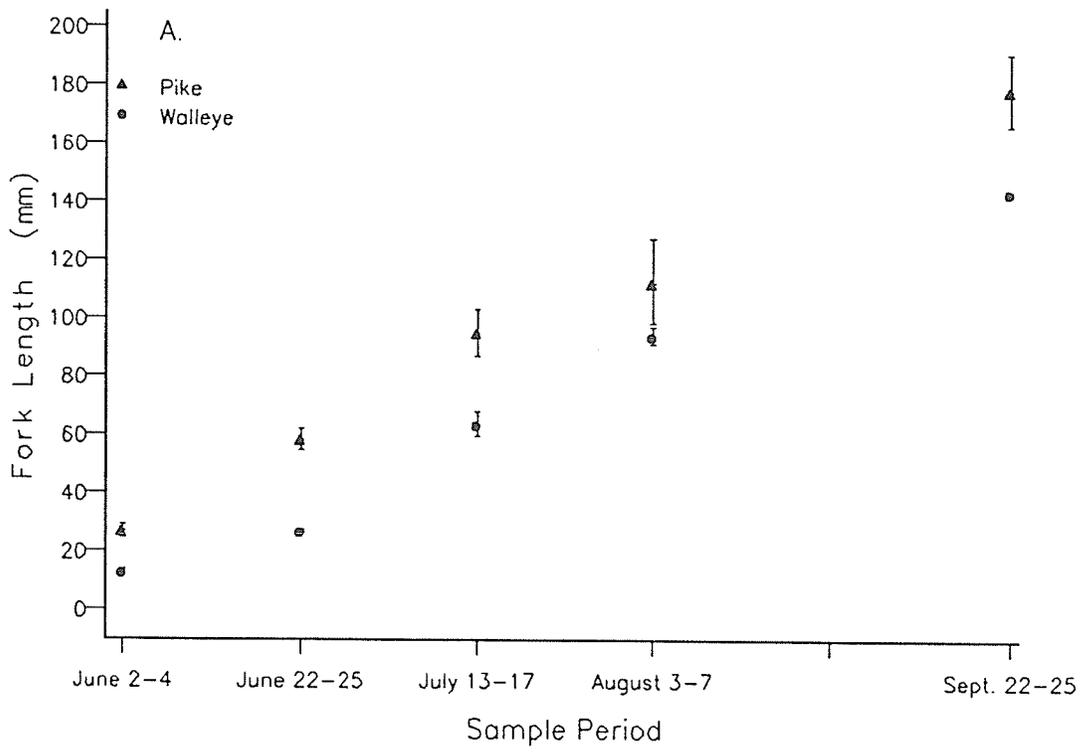
Ch. 1, Table 2. Fish species collected in Whitefish Lake during the summer of 1987.

Scientific Name	Common Name
<u>Catostomus commersoni</u>	White Sucker
<u>Coregonus artedii</u>	Cisco
<u>Coregonus clupeaformis</u>	Lake Whitefish
<u>Esox lucius</u>	Northern Pike
<u>Etheostoma exile</u>	Iowa Darter
<u>Etheostoma nigrum</u>	Johnny Darter
<u>Lota lota</u>	Burbot
<u>Notropis cornutus</u>	Common Shiner
<u>Notropis hudsonius</u>	Spottail Shiner
<u>Perca flavescens</u>	Yellow Perch
<u>Percina caprodes</u>	Log Perch
<u>Percopsis omiscomaycus</u>	Trout Perch
<u>Pimephales promelas</u>	Fathead Minnow
<u>Rhinichthys atratulus</u>	Blacknose Dace
<u>Rhinichthys cataractae</u>	Longnose Dace
<u>Stizostedion vitreum</u>	Walleye

Ch. I, Table 3. Sample sizes and re-transformed means for fork length (mm) and weight (g) of pike and walleye from each sample period. P-values are given for differences in mean size from t-tests using transformed data (fork length^{0.3}, log(weight)).

Variable	Sample Period	Northern Pike		Walleye		P-value
		n	mean	n	mean	
<u>Fork length</u>						
	June 2 - 4	17	26.7	12	12.8	0.0001
	June 22 - 25	27	58.3	15	27.0	0.0001
	July 13 - 17	9	94.9	7	63.6	0.0001
	August 3 - 7	9	112.2	11	94.1	0.004
	September 22 - 25	8	178.5	2	143.9	0.022
<u>Weight</u>						
	June 2 - 4	17	0.15	12	0.007	0.0001
	June 22 - 25	27	1.68	15	0.23	0.0001
	July 13 - 17	9	7.02	7	2.84	0.0001
	August 3 - 7	9	11.07	11	9.48	0.438
	September 22 - 25	8	47.10	2	36.02	0.403

Ch. I, Figure 3. (A). Mean fork length (mm \pm 95 % CI) and (B) weight (g \pm 95 % CI) of YOY pike and walleye collected in Whitefish Lake, June - September 1987. Sample periods were at three week intervals except the last two (six weeks apart). The confidence interval for walleye mean fork length and weight in September (n=2) was too large for the scale of the plot and is not illustrated.

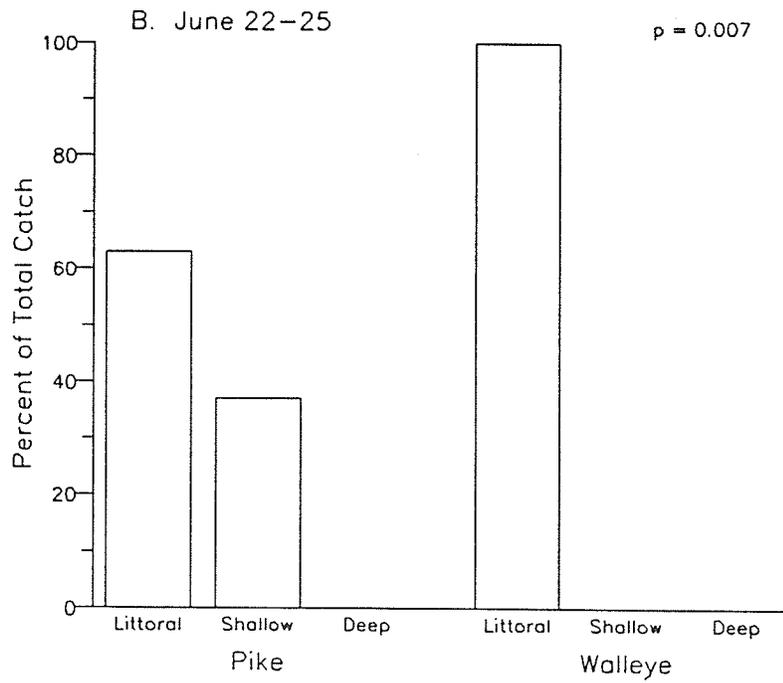
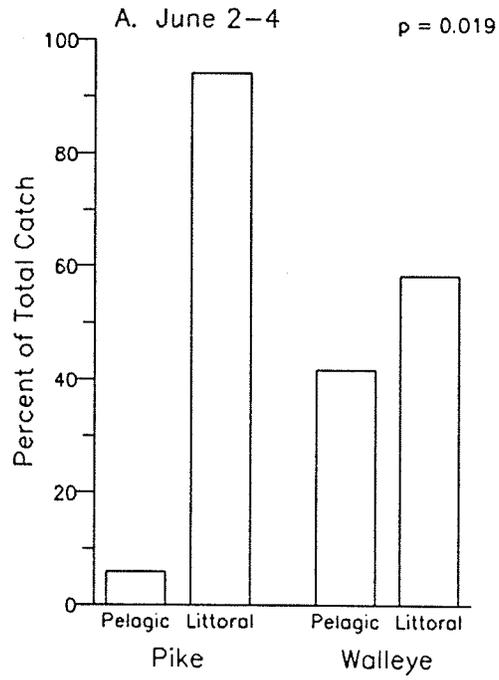


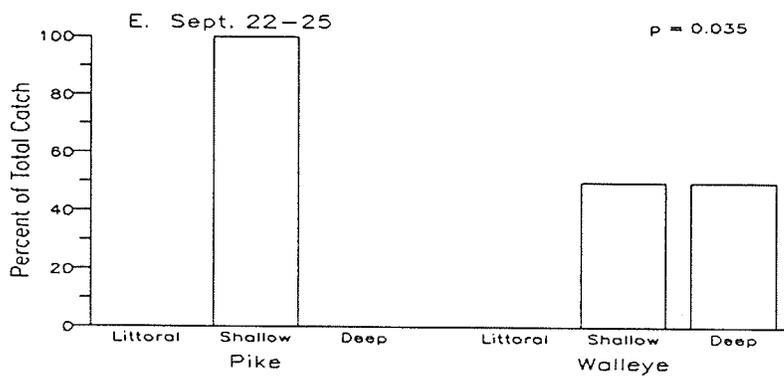
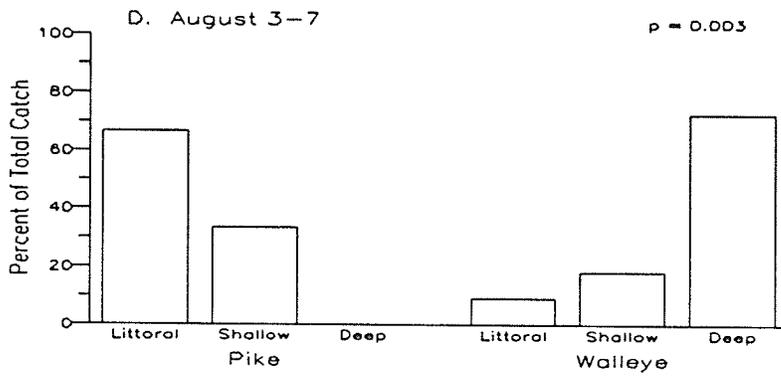
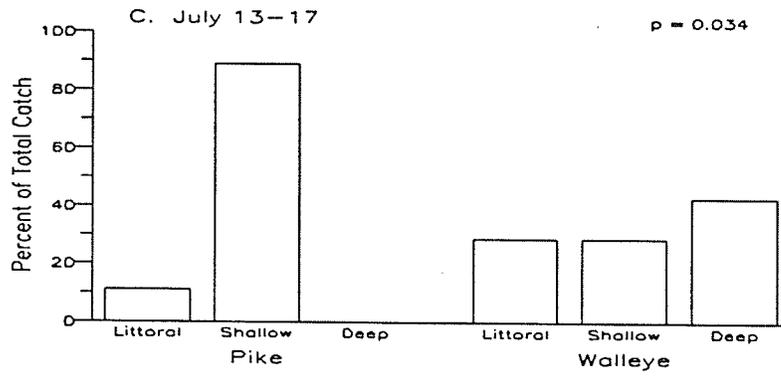
Habitat Use

Species distributions among the sampled habitats were significantly different in each sampling period (Fig. 4; chi-square contingency tests). The strong differences in distribution are partly due to low sample sizes however, since the presence or absence of one individual could markedly affect the proportions of fish in each habitat. Even with pooled samples, some of the expected frequencies were very small. In this situation, the chi-square approximation to the true distribution of the test statistic may be poor (Conover 1980). Therefore it is as important to evaluate which habitats were utilized by each species, by their presence and absence, as to statistically compare the relative proportions of catches in each.

In early June, the walleye were caught in the pelagic and littoral zones. Fish in the littoral zone were probably not demersal, but rather were also pelagic postlarvae, as indicated by their mean size at that time (12.8 mm). Their distribution was significantly different from that of pike which were almost all caught inshore in seine samples (Fig. 4). Species distribution was also significantly different in late June when walleye were found only in the shallow littoral zone whereas pike were collected both inshore and in the shallow offshore habitat (Fig. 4). Neither species was caught in the deep water otter trawls at any time of day in late June (Fig. 4). Both species occurred in seine hauls conducted at dawn, midday, and dusk in early and late June (Table 4). This, and the fact that the largest proportions of the catches of both species

Ch. I, Figure 4. Percentage of pike and walleye caught in each habitat zone (see text for description) during five sampling periods (A - E, as labelled). P-values are given for chi-square contingency tests of species differences in these proportions.





Ch. I, Table 4. Occurrence of pike and walleye in each habitat at each sampling time. Times of day are pooled in the combined presence/absence pattern shown at right. '+' = present; '-' = absent; 'NS' indicates areas not sampled.

Sample Period	Habitat	Dawn		Midday		Evening		Combined	
		NP	WE	NP	WE	NP	WE	NP	WE
June 2 - 4	Pelagic	+	+	NS	NS	-	+	+	+
	Littoral	+	+	+	+	+	+	+	+
June 22 - 25	Littoral	+	+	+	+	+	+	+	+
	Shallow	+	-	+	-	+	-	+	-
	Deep	-	-	-	-	-	-	-	-
July 13 - 17	Littoral	+	-	-	+	-	+	+	+
	Shallow	+	-	+	-	+	+	+	+
	Deep	-	-	-	+	-	+	-	+
August 3 - 7	Littoral	-	-	+	-	+	+	+	+
	Shallow	+	+	+	-	-	+	+	+
	Deep	-	-	-	+	-	+	-	+
September 22 - 25	Littoral	-	-	-	-	-	-	-	-
	Shallow	+	-	+	-	+	+	+	+
	Deep	-	-	-	-	-	+	-	+

were inshore together indicate that there was little temporal or spatial separation during these two time periods.

After late June, walleye were caught at dawn on only one occasion and on only three occasions at midday (Table 4). In late summer walleye occurred in the littoral habitat in only one evening sample (August); all other fish were collected in the offshore zone at various times of day (Table 4). It is therefore difficult to make any conclusions regarding their dawn and midday habitat use after midsummer, except to note that their use of the shallow, inshore habitat appeared to be restricted to the evening. Pike were somewhat more common; they occurred in the littoral and shallow offshore zones at all times of day throughout the summer (Table 4). Hence temporal differences in pike habitat use were not apparent.

Clearer patterns emerge from the evening samples, which are generally similar to those from the pooled data (Table 4). Walleye were captured in all three habitats in July and August evening samples, whereas pike were only in littoral and shallow offshore zones. The occurrence of walleye in the deeper offshore habitat resulted in their distribution being significantly different from that of pike in July and subsequent samples (Fig. 4). The general patterns illustrated in Figure 4 and Table 4 indicate that walleye moved offshore in late summer.

Conclusions regarding spatial and temporal distribution of pike and walleye are tentative since it should not be assumed that absence indicates non-use of an area, given the sparse data. Certainly the combined pattern shows that habitats are shared: there are only four times over the summer in which one habitat contained one species and not

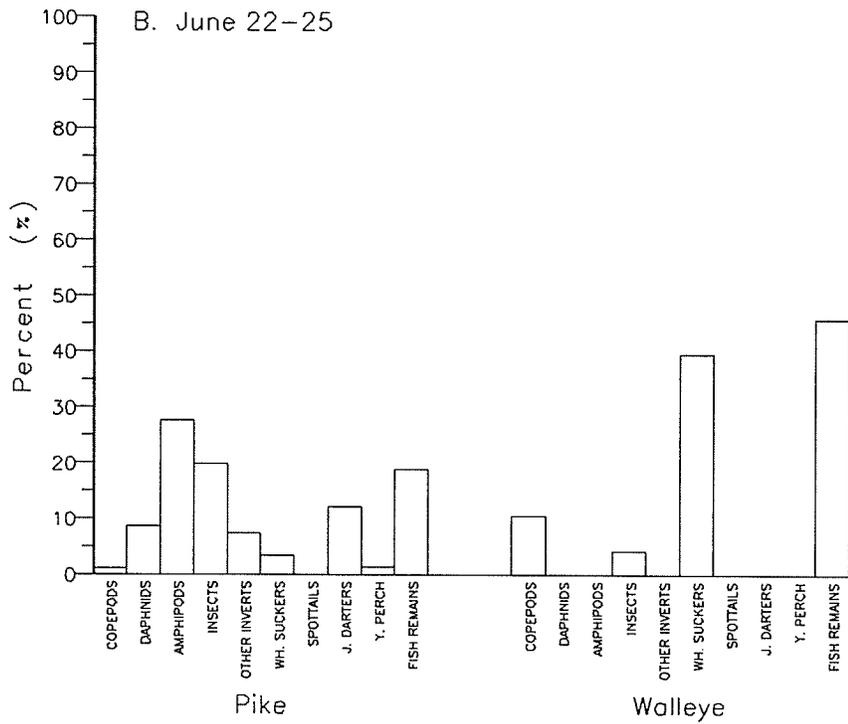
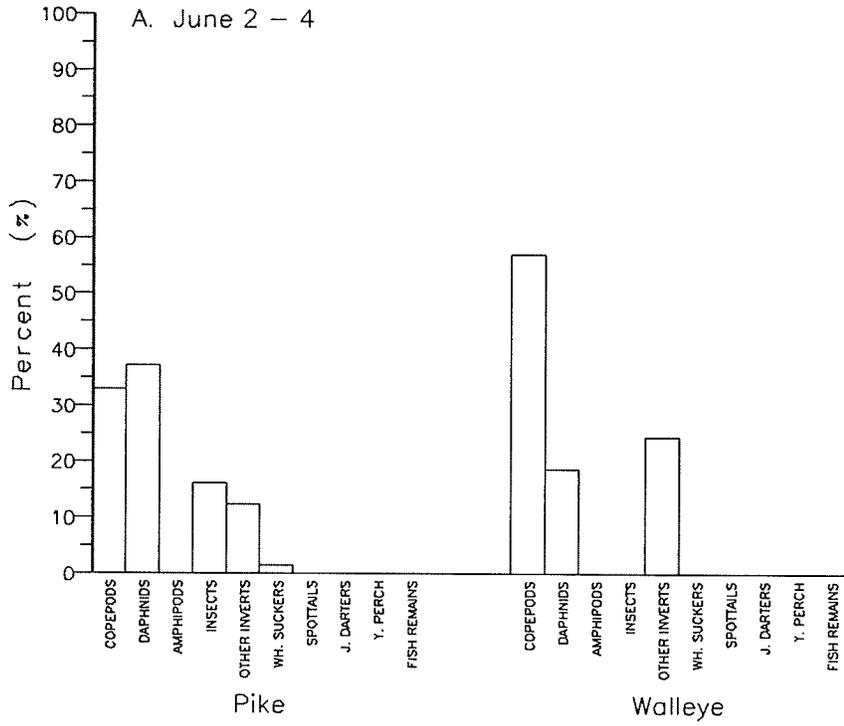
the other (Fig. 4; Table 4). The significant differences in species distribution indicate however that the importance of each of these habitats may be different for each species.

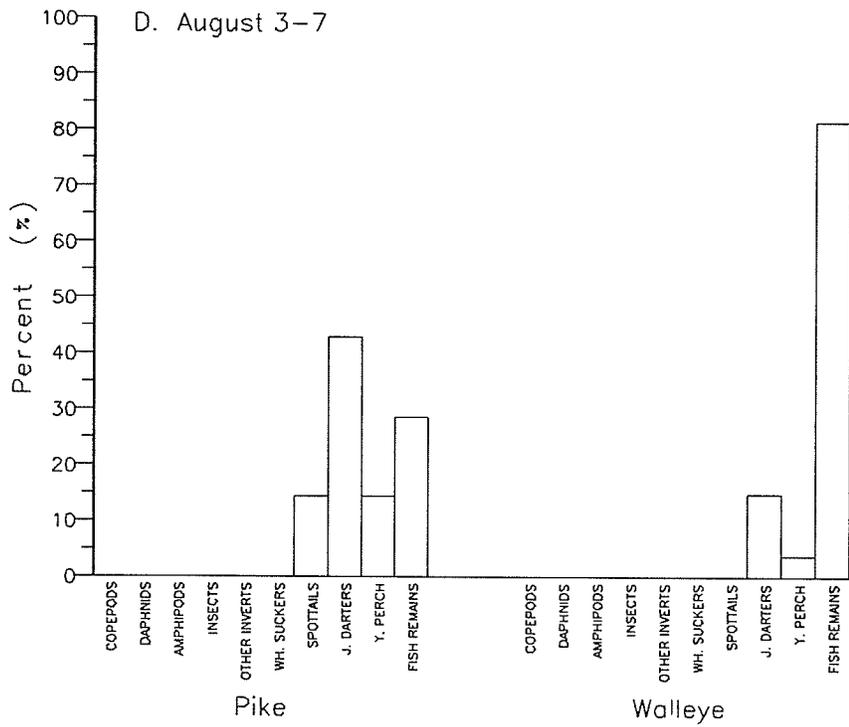
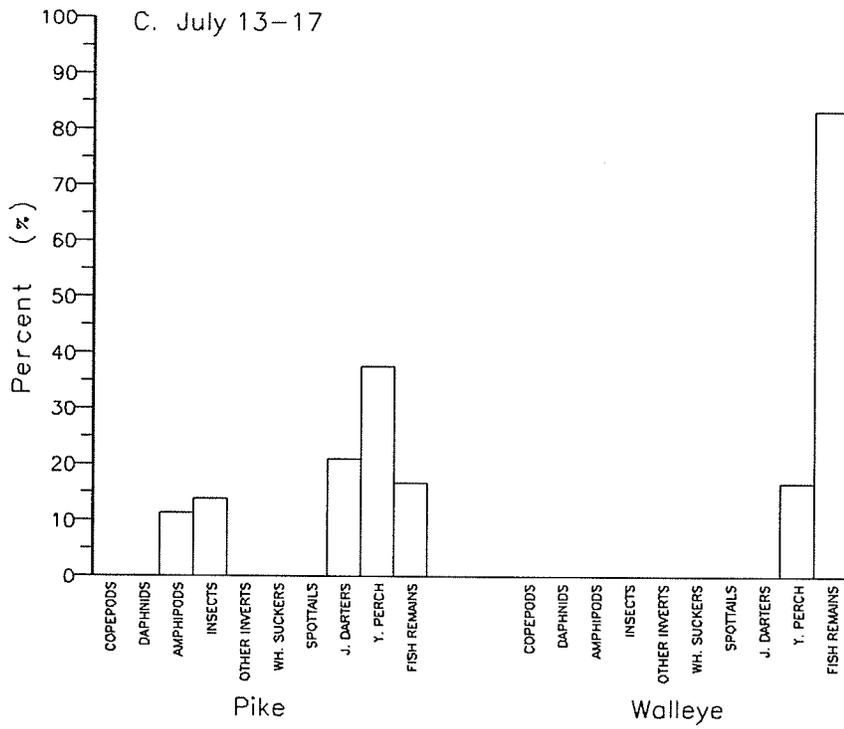
Food Use

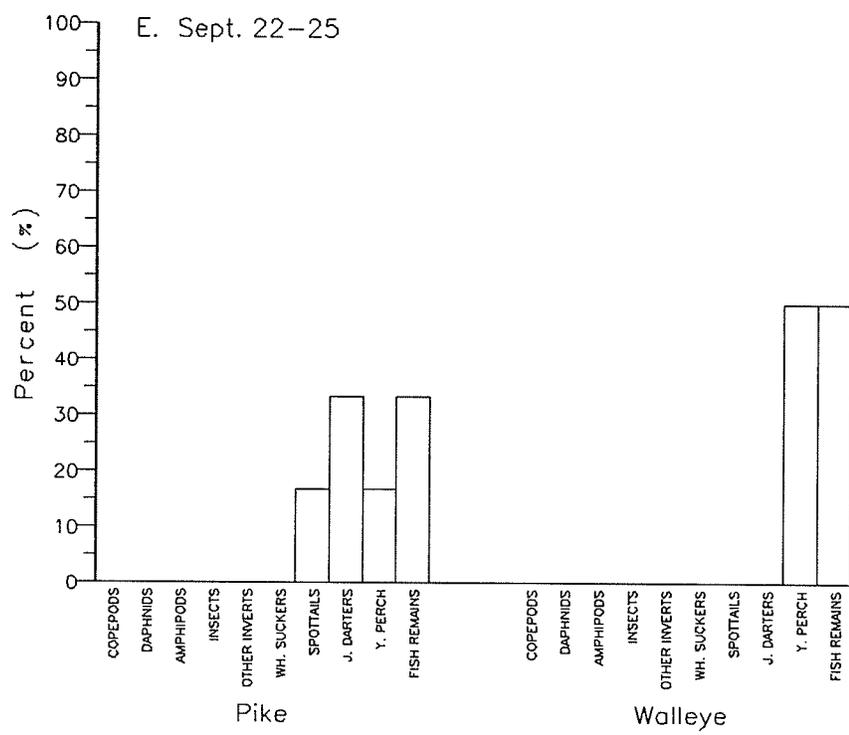
Types of prey items taken by pike and walleye were very similar throughout the summer. Each species underwent a gradual change from consuming zooplankton and macroinvertebrates in early June to consumption of small forage fish by late June (Fig. 5; Table 5). Most individuals contained food items, as indicated by the low occurrence of empty stomachs (Table 5). Prey size was not significantly different between pike and walleye (Table 6), despite the fact that pike were significantly longer in all samples (Table 3).

In early June, 70 to 80 % of the food items in pike and walleye stomachs were copepods and daphnids (Fig. 5A). Daphnids made up a smaller proportion of individual walleye diets than did copepods, and occurred in fewer stomachs than in pike. Larger items such as aquatic insects and other benthic invertebrates were found primarily in pike stomachs. The walleye, being much smaller, were almost totally zooplanktivorous. Invertebrates found in walleye stomachs, beside copepods and daphnids, were predominately other zooplankters. This was the only sample period during which mean prey lengths were close to being significantly different (Table 6), since only the pike were utilizing larger items at that time (Fig. 6A).

Ch. I, Figure 5. Proportions (%) of food items from pike and walleye stomachs that were in various prey categories. Proportions are based on numbers of items; results are illustrated for each of the five sample periods (A - E, as labelled).







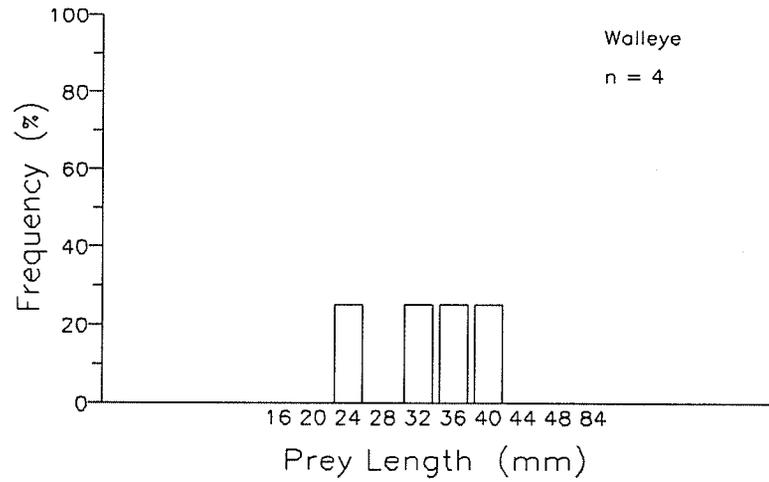
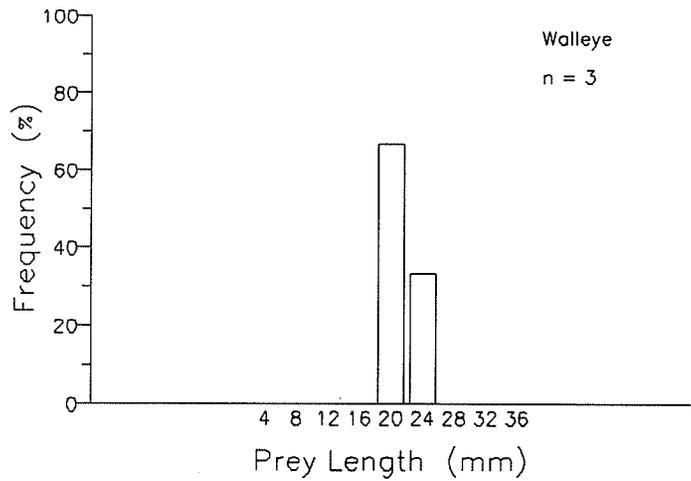
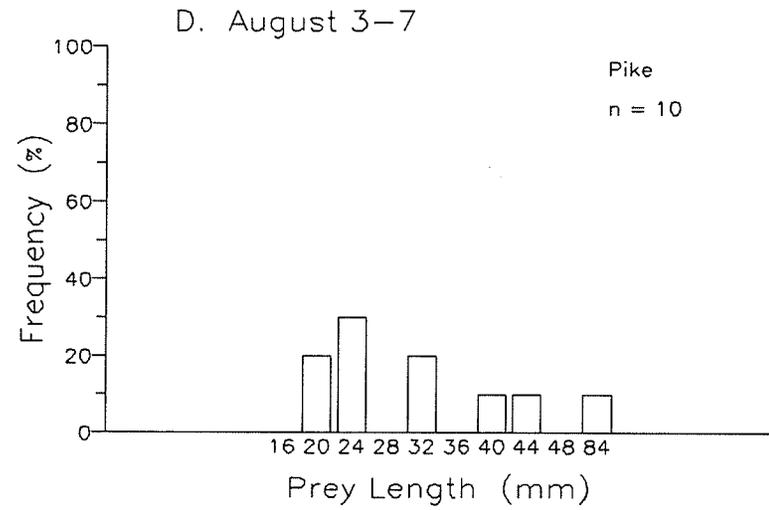
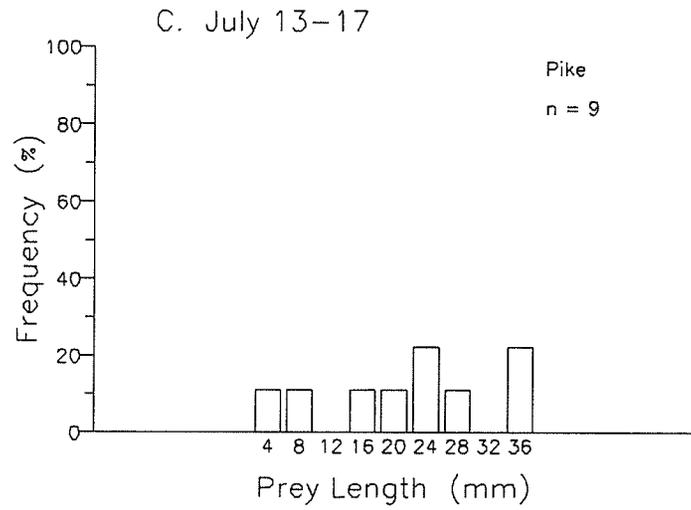
Ch. I, Table 5. Frequency of occurrence (% of fish) of various prey categories in pike (NP) and walleye (WE) stomachs from each sample period.

Prey Category	June 2 - 4		June 22-25		July 13-17		August 3-7		Sept. 22-25	
	NP	WE	NP	WE	NP	WE	NP	WE	NP	WE
Copepods	70.6	63.6	3.7	13.3	0.0	0.0	0.0	0.0	0.0	0.0
Daphnids	70.6	36.4	22.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipods	0.0	0.0	44.4	0.0	22.2	0.0	0.0	0.0	0.0	0.0
Insects	64.7	0.0	44.4	6.7	22.2	0.0	0.0	0.0	0.0	0.0
Other Inverts.	41.2	27.3	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
White Suckers	5.9	0.0	11.1	46.7	0.0	0.0	0.0	0.0	0.0	0.0
Johnny Darters	0.0	0.0	11.1	0.0	22.2	0.0	33.3	18.2	25.0	0.0
Spottail Shiners	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	12.5	0.0
Yellow Perch	0.0	0.0	3.7	0.0	33.3	14.3	11.1	9.1	12.5	100.0
Fish Remains	0.0	0.0	22.2	46.7	22.2	71.4	22.2	72.2	25.0	0.0
Empty Stomachs	0.0	9.1	7.4	20.0	11.1	14.3	22.2	18.2	25.0	0.0
No. of Stomachs	17	11	27	15	9	7	9	11	8	2

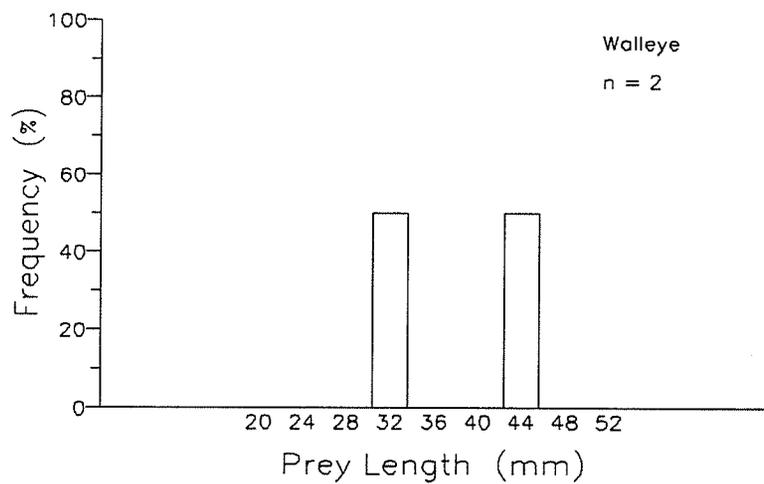
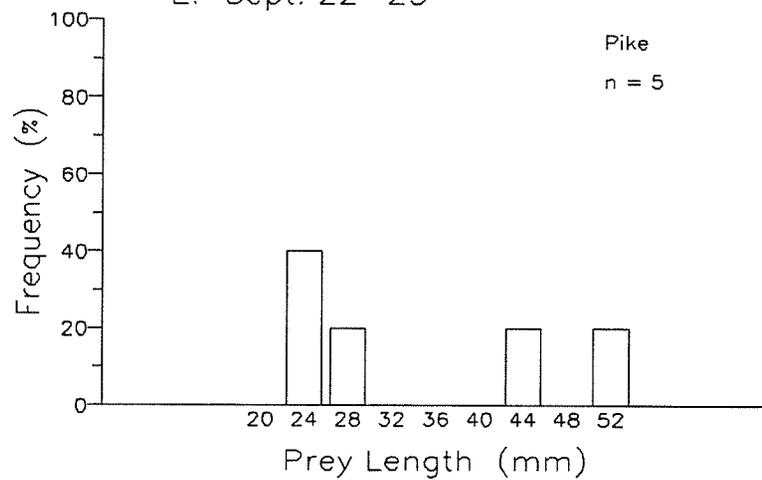
Ch. I, Table 6. Results of Mann-Whitney U-tests for differences in mean prey length between pike and walleye within each sample period. Numbers of stomachs are given in parentheses.

Sample Period	Mean length (mm) of ingested prey		P-value
	Pike	Walleye	
June 2 - 4	1.41 (16)	0.98 (8)	0.073
June 22 - 25	6.7 (23)	5.8 (6)	0.467
July 13 - 17	21.2 (6)	21.0 (3)	0.621
August 3 - 7	33.9 (6)	32.0 (3)	0.559
Sept. 22 - 25	34.2 (4)	37.5 (2)	0.907

Ch. I, Figure 6. Prey length frequency distributions (%) for prey items in pike and walleye stomachs from each sample period (A - E). N-values refer to numbers of prey items from which the distributions were calculated.



E. Sept. 22-25



By late June, small forage fish were an important component of both species' diets. The majority of prey items in walleye stomachs were either YOY white suckers or unidentified larval fish, though a few contained copepods or insects. In contrast, amphipods and other invertebrates still made up a significant proportion of the items in pike stomachs (Fig. 5B), and occurred in almost half the stomachs sampled (Table 5). Prey fish were generally larger in pike compared to walleye stomachs (Fig. 6B), so despite their lower occurrence, forage fish were probably as important for pike as for walleye. Both species had the widest diet breadth in late June, each taking prey items from a wide range of size and taxa. It therefore marks a period of transition from zooplanktivory to piscivory: zooplankton were not found in any fish collected later in the summer.

The mean sizes of prey found in pike and walleye stomachs in mid-July were almost identical (Table 6), although the range in prey size was greater for pike (Fig. 6C). This was partly due to very low sample size for walleye, but also because some pike were still consuming invertebrates, whereas the sampled walleye were not (Table 5; Fig. 5C). Most of the fish in walleye stomachs were too digested to identify or measure, but were similar in size to the yellow perch found in some walleye and pike.

In August and September samples the pike and walleye were entirely piscivorous (Fig. 5D-E; Table 5). It is difficult to assess which prey species were more prevalent because so many consumed fish could not be identified. Furthermore, only two walleye were collected in September; each contained only one fish. Very few prey items were identified and

measured in these sample periods, but those that were indicate that pike and walleye preyed on similar sizes of the same fish species (Figs. 5D-E, 6D-E).

DISCUSSION

Overall patterns of food use, and temporal and spatial distribution of YOY pike and walleye were similar. The greatest degree of habitat overlap appeared to be during the early summer, when both species were primarily in the shallow littoral zone. Walleye caught in early June were probably still pelagic postlarvae, as indicated by their small size, zooplanktivorous diet, and their greater susceptibility than pike to the bongo nets. I expected that pike would be feeding on larger prey items, based on their larger size, but this was not the case. Aquatic insects and other macroinvertebrates were an important component of the pike diet, but zooplankton were still numerically prevalent as well.

Walleye are thought to move inshore to feed by about 25-30 mm total length as they change from pelagic zooplanktivores to demersal predators on benthos and then fish (Bulkley et al. 1976). The evidence from this study was in agreement: walleye caught inshore in late June (mean size 27.0 mm) were preying on small forage fish and some invertebrates. Based on their size (58 mm), pike were also expected to have switched to piscivory, but invertebrates were still prevalent in pike stomachs in late June. The higher energetic return associated with larger food items (Kerr 1971) and with fish versus invertebrate prey

(Knight et al. 1984) both imply that pike may have been experiencing some degree of food limitation during this period, since small fish seemed readily available.

The co-occurrence of YOY pike and walleye in the littoral zone of Whitefish Lake, and the lack of any temporal separation in their use of this habitat indicate an overlap in habitat during early summer. The littoral zone was probably an important habitat for both species for a number of reasons. Small fish species and the smaller size classes of larger fish are often restricted to shallow, vegetated, inshore areas because of the availability of cover for predator avoidance (Werner et al. 1983; Tonn and Paszkowski 1987). As 'sit-and-wait' ambush predators, pike also require cover for concealment from their own prey. Prey availability may also have been highest in this habitat. Catches of small forage fish species were generally lowest in the offshore zone, and other studies have shown that benthic invertebrate abundance is usually lowest in the open water area as well (Wetzel 1983; Persson 1986). The similarities in food use and the inshore co-occurrence of YOY pike and walleye during early summer provide evidence of a potential for competition.

After late June, walleye were collected in the deeper offshore zone during each sampling period, whereas pike did not occur there at any time. In July the walleye showed the widest range of habitat use (Fig. 4), indicating that they were changing to an offshore distribution at that time. Previous studies have detected the same shift but have differed widely in their estimates of when it occurs (Forney 1966; Johnson 1969; Ryder 1977; Johnson et al. 1988). The move offshore is

probably related to changes in the rod cells and tapetum of the walleye eye that greatly increase its sensitivity to light. This occurs at total lengths of about 60-70 mm (Braekevelt et al. 1989), which compares well with the size of walleye sampled in July (mean fork length 63.6 mm). One might expect that the migration be accompanied by an increased susceptibility to predation because of the reduced availability of cover offshore. Predation among fish species is usually size dependent (Werner 1986; Post and Evans 1989a), so perhaps the size at which tapetum development causes walleye to move offshore is related to a size dependent decrease in susceptibility to predation. In addition, negatively phototactic walleye are inactive during the day and usually rest on the lake bottom (Ryder 1977), thereby reducing their vulnerability to diurnal piscivores. Their movement inshore at twilight may also allow them to avoid crepuscular predators feeding offshore, such as larger walleye.

In contrast, pike remained inshore throughout the summer. Their requirement of aquatic vegetation for cover from prey and for spawning partly explains why they utilize shallow, weedy habitats throughout their life. A number of studies have inferred that pike biomass is related to littoral macrophyte abundance. Forney (1977) and Colby et al. (1987) suggested that the decline in pike abundance in some lakes was a consequence of the removal of inshore aquatic vegetation.

The differences in distribution of pike and walleye in mid to late summer indicate that the potential for competition may be reduced among older YOY fish. However there are a number of reasons why this may not be the case. First, both species occurred in the shallow offshore zone

during the three mid to late summer sampling periods. This 2-3 m deep zone bordered with the shallow littoral zone sampled by seine and therefore the two areas may not have been recognized as distinct habitats by the fish. This seems likely given that both areas contained submersed vegetation and that a similar variety of forage fish species occurred in each. This illustrates the problem of making studies of habitat differences with fish that have been collected rather than observed. It is difficult to subdivide habitat using criteria that can be assumed to be meaningful to the fish. Fine scale habitat differences were undetectable by the methods used, and this may have contributed to the apparent similarities in habitat distribution of pike and walleye.

The potential for competition may also still be significant despite habitat differences because pike and walleye were consuming similar sizes of the same prey fish species during mid to late summer. Most of the identified prey taxa occurred in both pike and walleye stomachs within the same sampling period. Prey fish were generally YOY and therefore each species was of a narrow size range. As a result there was considerable overlap in the size range of prey items consumed by pike and walleye, despite the interspecific differences in their own sizes.

Habitat segregation does not always preclude competition if individuals utilize mobile prey (Holt 1987). Pike may be specialized to live in the inshore littoral habitat but they may reduce the numbers and hence the movement of forage fish into the offshore zone occupied by walleye (or vice versa). Therefore an effect may be caused in the absence of any contact between competing species. In addition, there was

limited evidence from this study that negatively phototactic walleye moved inshore to feed in the evening. Other research has shown this to be the case (Ryder 1977; Serns 1982b; Ryder and Kerr 1978). This would have increased the likelihood that YOY pike and walleye were sharing the food resource. Differences in feeding periodicity may reduce contact between the species, but will not prevent exploitative competition (Holt 1987).

One unexpected result from this study was the consumption of invertebrates by pike in late June and mid July. The mean fork length of pike was 98 mm by the latter sampling period, well past the size at which pike have been shown to be primarily piscivorous (Hunt and Carbine 1951; Frost 1954; pers. observ.). The conversion from an invertebrate to fish diet is necessary at a small size for juvenile piscivores, since they require prey of increasing size and energy value to maintain growth (Kerr 1971; Hurley 1986). The growth rate of pike appeared to be reduced in the interval between late June and early August, and differences in pike and walleye size became less pronounced by late summer (Fig. 3). Cooler temperatures can not explain this finding because YOY walleye and pike have similar optimal temperatures for growth (24°C and 26°C respectively; Bevelheimer et al. 1983; Hokanson and Koenst 1986), and the walleye did not exhibit the same reduction. Growth may therefore have been limited by prey quantity or quality, given that pike were utilizing invertebrate prey. Pike and walleye are both opportunistic predators, selecting prey on the basis of their size and relative abundance (Beyerle and Williams 1968; Knight et al. 1984; Chapman et al. 1989), but given the pike's size, consumption of invertebrate prey was

presumably less energy efficient, as noted earlier. Walleye were only consuming forage fish by mid July and their growth pattern did not suggest any food limitation. The results suggest that the walleye caught up to the pike by late summer both in body size and in the mean size of their prey (Fig. 3, Table 6). It is possible that walleye feeding inshore had an effect on prey availability for pike, although intraspecific interactions or unrelated abiotic and biotic factors may have been just as important an influence on the food supply. The assumption that the stomach contents of fish that I examined were representative of the total population must be viewed with caution because sample sizes were small.

I have avoided drawing conclusions regarding the existence of competition between these species from the results of this study. This would require a demonstration that growth and survival are limited by resource availability and that one species uses some resource in a manner that makes it limiting for the other species (Grant 1986). The coexistence of pike and walleye in Whitefish Lake does imply that there is insufficient niche overlap and resource limitation for competition to cause the exclusion of pike or walleye. Although overlap was demonstrated, the distribution of YOY fish among the habitats showed that the importance of each habitat was different for each species. This, and the feeding flexibility exhibited by pike and walleye (Knight et al. 1984; Chapman et al. 1989; this study), probably play a role in their ability to coexist. Competition may still have an important effect on YOY cohort strength however, since reduced growth resulting from exploitative competition can lead to size-dependent starvation and predation

mortality. Competition may also be more important in smaller lakes where more homogeneous habitat results in stronger interactions, as demonstrated with a few other fish assemblages (Werner and Hall 1977; Tonn and Paszkowski 1987). Johnson et al. (1977) stated that the low occurrence of walleye-only lakes and the larger mean size (244 ha) of pike-walleye lakes in Ontario was perhaps because of a low probability of pike and walleye coexistence in smaller lakes. Coexistence of pike and walleye in Whitefish Lake (675 ha) could therefore be related to its size and by association, its degree of habitat heterogeneity.

Conclusions

The purpose of this study was to assess the degree of overlap in resource use by YOY pike and walleye. Basic similarities were demonstrated in both habitat and food use, although the degree of overlap changed over the course of the summer. My research adds to the information already available because I directly compared YOY resource use in a lake in which pike and walleye exist together. Therefore, the conclusion from my results is that pike and walleye do exhibit a potential to compete during their first summer.

Low catches of fish made quantitative comparisons of pike and walleye resource use difficult. A considerable amount of sampling effort yielded a limited amount of information. As a result, I decided not to repeat the study in subsequent summers. Furthermore, Whitefish Lake can obviously not be considered representative of all lakes in which both pike and walleye exist, although I think that the results are still

useful because of the comparative nature of this study. A comparison of populations from different lakes would be informative, as would a long-term investigation of resource use patterns, but the sampling effort and time required for such studies were not available. I felt that it would be more profitable to concentrate on more direct means of investigating competition. The following two chapters of this thesis present the results from experimental work.

CHAPTER II:
Intraspecific versus interspecific competition among
young-of-the-year northern pike and walleye:
evidence from an enclosure experiment

INTRODUCTION

Competition has been suggested to be a major selective force in freshwater fish communities (Larkin 1956; Ross 1986; Werner 1986). Competitive interactions at a specific life stage can significantly affect the dynamics and size structure of whole populations by restricting recruitment to the next size class (Persson 1986; Werner 1986). For example, competition between young-of-the-year (YOY) fish may be an important influence on their growth and survival, and hence on cohort strength. Year class abundance of northern pike and walleye populations are thought to be determined during the YOY stage, but the role of competition has not been directly examined. Rather, competition between these species has been suggested on the basis of indirect evidence.

Overlap in resource use has often been used as evidence of competition between pike and walleye (Swenson and Smith 1976; Forney 1977; Craig and Smiley 1986). Sympatric and allopatric populations of potential competitors have often been compared in an effort to detect niche shifts that would be circumstantial evidence of competition (eg. Schmitt and Coyer 1983; Tonn and Paszkowski 1987; Hindar et al. 1988). Changes in relative population abundance following species introductions and removals are also often attributed to competition (eg. Swenson and Smith 1976; Anthony and Jorgensen 1977; Forney 1977; Johnson 1977; Persson 1983; Persson 1986; Colby et al. 1987). Manipulations involving the stocking of YOY pike and walleye have showed consistent evidence for competitive interactions (Wesloh and Olson 1962; Colby et al. 1987), as described in the general introduction.

The majority of natural experiments suffer from lack of replication and controls, making it difficult to determine whether a niche shift or changes in abundance are not simply a consequence of other factors such as the abiotic environment or predation (Diamond 1986). Still, there have been many different studies of allopatric and sympatric populations and of species introduction and removal 'experiments' with consistent results. This lends strength to the overall conclusion that competition was an important mechanism governing the observed changes in population abundance, growth rates, and resource use patterns.

The most convincing evidence for competition comes from manipulative field experiments (Schoener 1983; Connell 1983; Fausch 1988). A properly designed field experiment will separate the effects of interspecific competition from that of intraspecific competition (Connell 1983). It is not sufficient to assess whether adding or removing the potential competitor has an effect on a species, because the possibility that an addition or removal of conspecifics could have the same effect has not been assessed. In other words, intraspecific competition could be equal to or stronger than interspecific competition (Connell 1983).

Field experiments have been conducted for a few freshwater fish species, but most suffer from a combination of incomplete design, lack of proper replication, or unnatural experimental conditions. Werner and Hall (1977; 1979) studied competitive interactions among three sunfish species (Lepomis spp.) in pond enclosures. Unnaturally high fish densities were used and some experiments lacked controls, making their applicability to natural populations questionable. Clady and Luker

(1982) found no evidence of competition when natural densities of two species of bass (Micropterus salmoides and M. punctulatus) were stocked into pond enclosures. Persson (1987a; 1987b) used natural biomasses of perch (Perca fluviatilis) and roach (Rutilus rutilus) in lake enclosures, but did not use enough treatments to compare intraspecific and interspecific effects, nor were the treatments replicated. Hanson and Leggett (1985; 1986) compared intra- and interspecific competition between yellow perch (Perca flavescens) and pumpkinseed (Lepomis gibbosus) with a well designed but unreplicated enclosure experiment. These experiments also showed that competition may be important in freshwater fish communities, but their shortcomings illustrate the need for better experimental design.

No experimental evidence exists to demonstrate competition between YOY pike and walleye. The indirect evidence outlined above, and the direct comparison of YOY pike and walleye habitat and food use made in the preceding chapter indicate that there is a potential for them to compete. In this chapter I examine competitive interactions between these species by use of a replicated field experiment designed to detect and compare intra- and interspecific competition. Specifically, the aim of this experiment was to test the hypothesis that YOY pike and walleye compete when food-limited. This was done by manipulating fish density and prey availability in enclosures that simulated natural conditions as much as possible. Competition would be demonstrated by reduced fitness (as measured by growth and survival) that is clearly a consequence of either species' effect on conspecifics or the other species. A further aim was to test for effects on food resource utilization, since

diet shifts provide circumstantial evidence for competitive interactions (Diamond 1986; Hanson and Leggett 1986).

MATERIALS AND METHODS

Study Area

I conducted the experiments at the Department of Fisheries and Oceans Dauphin Lake Walleye Rehabilitation and Research Centre at Methley Beach, Manitoba ($51^{\circ} 17' N$, $99^{\circ} 48' W$; Chapter I, Fig. 1). A small pond was used for the enclosure experiments. It was 0.14 ha in area and had a maximum depth of approximately 2 m. All enclosures were installed at a depth of 1 m. The abundance of submersed vegetation at this depth varied around the pond from sparse bottom cover to complete cover with plants reaching mid depth in height. This factor was considered in the experimental design and layout for the enclosures.

Experimental Design

I used an experimental design with the minimum number of treatments needed to detect and compare the direction and intensity of intraspecific and interspecific competition between pike and walleye (Underwood 1986; Table 1). The hypothesis is that competition occurs when fish are food limited. Therefore per-capita food availability was varied between treatments by manipulating single species density between

Ch. II, Table 1. Experimental design to test for intra- and inter-specific competition in the pond enclosures (from Underwood 1986). Numbers refer to enclosure densities of each species.

Species	Treatment				
	1	2	3	4	5
Northern pike	10	5	5		
Walleye			5	5	10

a low and high level while all treatments received the same total daily provision of forage fish. Reduced growth or survival for a species in the high compared to the low density treatment would indicate intraspecific competition. Interspecific competition was tested by comparing the outcome in the mixed species case and the high density case against the low density treatment for a given species. With pike for example, the effect of adding 5 walleye to 5 pike was compared to the effect of adding 5 pike to 5 conspecifics. Interspecific competition is demonstrated when these effects differ, the dominant species being the one which has better growth and survival with the other species than with its own.

The lower density of fish (5 per enclosure) was chosen so as to be high enough that total production would be insensitive to individual mortalities yet not so high that total biomass was unnaturally high. The enclosure biomass of pike and walleye probably exceeded natural densities for each of these species, but this is justified as follows. The biomass of the total littoral fish community (all species) under natural conditions is considered independent of the number of species and is often correlated with nutrient levels or macrobenthos biomass (Hanson and Leggett 1982). Therefore it is reasonable that the simplified system within enclosures without other fish species could support a biomass of experimental fish that alone equals a natural total littoral fish community biomass. The validity of this and other assumptions concerning enclosure conditions will form part of the discussion.

The experiment was performed in duplicate in 1987 on two occasions and in triplicate in 1988 on three occasions. Experimental units (the

enclosures) were blocked on each side of the pond because of differences in macrophyte abundance. It was thought that cover provided by macrophytes could affect prey capture and hence fish growth. A blocked design ensured that each treatment occurred only once on each side of the pond. The treatments were randomly assigned to enclosures within each block before commencing a trial.

Materials

The frame of the enclosures (1.5 m x 2.0 m x 1.2 m) was constructed from 3.75 cm x 3.75 cm lumber. Sides were covered by 1.3 mm mesh fiberglass window screening. A 30 cm wide skirt of reinforced plastic sheeting was attached around the lower edge of the frame. Enclosures were placed in approximately 1 m of water and tied to two stakes driven into the substrate at opposite corners. Sandbags were placed on the bottom skirt to ensure that the lower edge was sealed. A section of gillnetting covered each enclosure to keep out birds. The enclosures were installed in both years at least three weeks before experiments began.

Pike used in the first trial in 1987 were donated by the Wisconsin Department of Natural Resources Wild Rose Hatchery. Fish for the second trial and for 1988 trials were collected by seining along a weedy bank of the Turtle River, approximately 2 km upstream from where it flows into Dauphin Lake. I collected walleye in trap nets set in the rearing ponds at the Methley Beach Research Station in both years.

Procedure

All pike and walleye were collected at least three days before a trial and held in 120 l aquaria in a laboratory or in holding pens in the enclosure pond. The fish were fed ad libitum with live fish until one day before a trial commenced. Forage fish were then removed and the experimental fish were deprived of food for 12-24 hours (the longer period for larger fish in later trials). This ensured that the fish had empty stomachs at the start of a trial and therefore all weight gain could be considered a product of food consumed during the experiment.

On the first day of each trial, groups of 10-15 experimental fish were anaesthetized in an aerated MS-222 solution (approximately $75 \text{ mg}\cdot\text{l}^{-1}$), one group at a time. Fish were marked for all trials except the first in 1987. Individual marks were made by branding with a flamed wire loop at different locations just above the lateral line. Each fish was measured (fork length $\pm 1 \text{ mm}$) and weighed (blotted wet weight $\pm 0.1 \text{ g}$) before being introduced into appropriate enclosures. The procedure required 4-5 hours to complete. Fish were assigned so that each enclosure population, as much as possible, contained a representative size range of fish.

In 1987 the two trials were of 7 and 9 days duration. The three trials in 1988 were of 14 days duration. Forage fish were provided daily during each trial between 16:00 and 18:00. I also made visual observations on the experimental fish when conditions permitted and checked the condition of the enclosures at this time. If dead fish were observed they were removed and identified. Water temperature of the pond was

measured daily with a YSI Tele-Thermometer in 1987, and continuously with two Peabody Ryan Model J-180 thermograph recorders in 1988.

I estimated how much forage fish to provide using a daily ration of 10 - 25 % of the mean initial weight of experimental fish. This value varied among but not within trials (Table 2). The value was reduced in 1988 because I concluded it had been too high in 1987, for reasons that will be explained later. The total ration (g) for 5 fish (the low density treatment) was calculated using the mean initial weight pooled for both species in 1987 and separate estimates for pike and walleye in 1988. This was because initial weights of the 2 species were significantly different in 1988 trials. Using separate values ensured that the ration was the same for both species on a percent body weight per day basis. The mean wet weight of forage fish was also estimated to enable conversion of the calculated daily ration weight to numbers of forage fish. This number was provided to all enclosures, so that per-capita forage fish availability was reduced in high density and mixed species treatments. Forage fish species varied among trials and depended on availability (Table 2).

At the end of each trial experimental fish that had survived were removed with a small seine and killed in a strong solution of MS-222 to prevent regurgitation of stomach contents. Individuals were identified, measured, and weighed before preservation. Food items in each stomach were identified and enumerated at a later date. Items were grouped into the following categories: the various fish species, daphnids, other Cladocera, calanoid Copepoda, cyclopoid Copepoda, Amphipoda, Odonata naiads, Ephemeroptera nymphs, Corixidae, Chironimidae, other Diptera,

Ch. II, Table 2. Schedule and details of enclosure experiments conducted during 1987 and 1988. Total mortality includes both unexplained losses and those accounted for during each trial. Percent mortality is based on an initial number of 40 pike or walleye in 1987 and 60 of each in 1988. YOY = young-of-the-year.

Trial Date	Duration (days)	Ration (% initial body weight per day)	Forage Fish Species	Total Mortality (%)	
				Pike	Walleye
July 22 - July 29/1987	7	25 %	YOY <u>Perca flavescens</u>	10.0	42.5
August 7 - August 17/1987	10	25 %	<u>Culaea inconstans</u>	0.0	0.0
June 28 - July 12/1988	14	15 %	YOY <u>Pimephales promelas</u>	26.7	36.7
July 19 - August 2/1988	14	10 %	YOY <u>Notropis hudsonius</u> & <u>N. atherinoides</u>	6.7	20.0
August 9 - August 23/1988	14	10 %	YOY <u>Pimephales promelas</u>	5.0	0.0

and other Insecta. Stomach fullness was assessed on an arbitrary scale from 0 to 3 (0 = empty to $\frac{1}{4}$ full; 1 = $\frac{1}{4}$ to $\frac{1}{2}$ full; 2 = $\frac{1}{2}$ to $\frac{3}{4}$ full; 3 = $\frac{3}{4}$ to full).

Analyses

If stomach contents weighed more than 5 % of an individual fish's total final weight then the amount was subtracted from the final weight before further calculations. Initial mean weights of each species of experimental fish were compared by ANOVA. I also tested for differences in mean initial weight among the five trials, for each species. The range in total enclosure biomass among treatments was calculated for each trial to assess whether it exceeded values of estimated total littoral fish biomass found in the literature.

The proportion of experimental fish surviving in each enclosure was calculated and the values transformed (arcsin square-root) to stabilize the variance. ANOVA was used to test for differences in mean survival between treatments and between species, in each trial.

Estimates of production were used to assess the direction and intensity of competitive interactions. Production is a measure of the total elaboration of tissue during a time interval, including that produced by fish which die during the interval. It is therefore sensitive to both growth and survival, either of which could be affected by

competition. Production in each enclosure was calculated using the equation :

$$P = (G \cdot \bar{B}) / (N_1 \cdot \bar{W}_1), \quad (1)$$

where G is instantaneous growth rate, $\ln(\bar{W}_2) - \ln(\bar{W}_1)$, \bar{B} is average biomass over the interval, $(B_1 + B_2) / 2$, N_1 is the initial number of experimental fish, and \bar{W}_1 and \bar{W}_2 are mean fish weight in an enclosure at the start and end of an interval, respectively. This is modified from the usual equation $P = G \cdot \bar{B}$ (Chapman 1978). The two components of the denominator standardized enclosure production for comparisons between treatments with different numbers and initial sizes of fish. Hence total production for each enclosure was expressed by grams produced per gram initial weight. I tested for intraspecific and interspecific competition by comparing mean enclosure production using ANOVA for a blocked design. Six non-orthogonal comparisons (one degree of freedom each) were chosen a priori. These were: an overall comparison of mean production between pike and walleye, comparisons between low and high density enclosures for each species (testing intraspecific competition), each species' mean production in high density versus mixed species enclosures, and lastly, pike versus walleye mean production in mixed species enclosures. The Dunn-Sidak method was used to adjust each test to a significance level of $\alpha' = 1 - (1 - \alpha)^{k-1}$ for an experimentwise error rate $\leq \alpha$ for k contrasts (Sokal and Rohlf 1981). I calculated α' and corresponding critical F values for three levels of significance so that relative P-

values could be determined for each comparison. Values of α' for $\alpha = 0.10, 0.05, \text{ and } 0.01$ were $0.0174, 0.0085, \text{ and } 0.0017$, respectively. This adjustment of the critical F makes the tests very conservative; individual contrasts are much less likely to be declared significant. However it is more appropriate than a posteriori methods that test unplanned comparisons indicated by the data, since only certain comparisons were of interest in this experiment.

Experimental fish were classified into a 4×6 contingency table for an analysis of stomach fullness. Columns were the six treatment categories and rows were the four levels of the stomach fullness index. Data from different blocks were first pooled within each treatment to increase sample size. The null hypothesis was that the distribution of fish stomach fullness values was identical for all treatment populations. This was tested using the Kruskal-Wallis ranks test (K-W test) for contingency tables, where rows represent ordered categories (stomach fullness values), and columns represent different populations. This method utilizes more information contained in the data and provides a more powerful test than a chi-square contingency test in which both rows and columns are categorized only on a nominal scale (Conover 1980).

Food items in the stomachs of experimental fish were classified into broad groupings: zooplankton, amphipods, aquatic insects, and forage fish. Frequency of occurrence was calculated as the percentage of stomach samples in each treatment group containing one or more items of a given food type. Although insensitive to relative abundances of each food type (Windell and Bowen 1978), this measure was assumed to be

representative of diet breadth because usually one food type dominated the stomach contents in both numbers and volume.

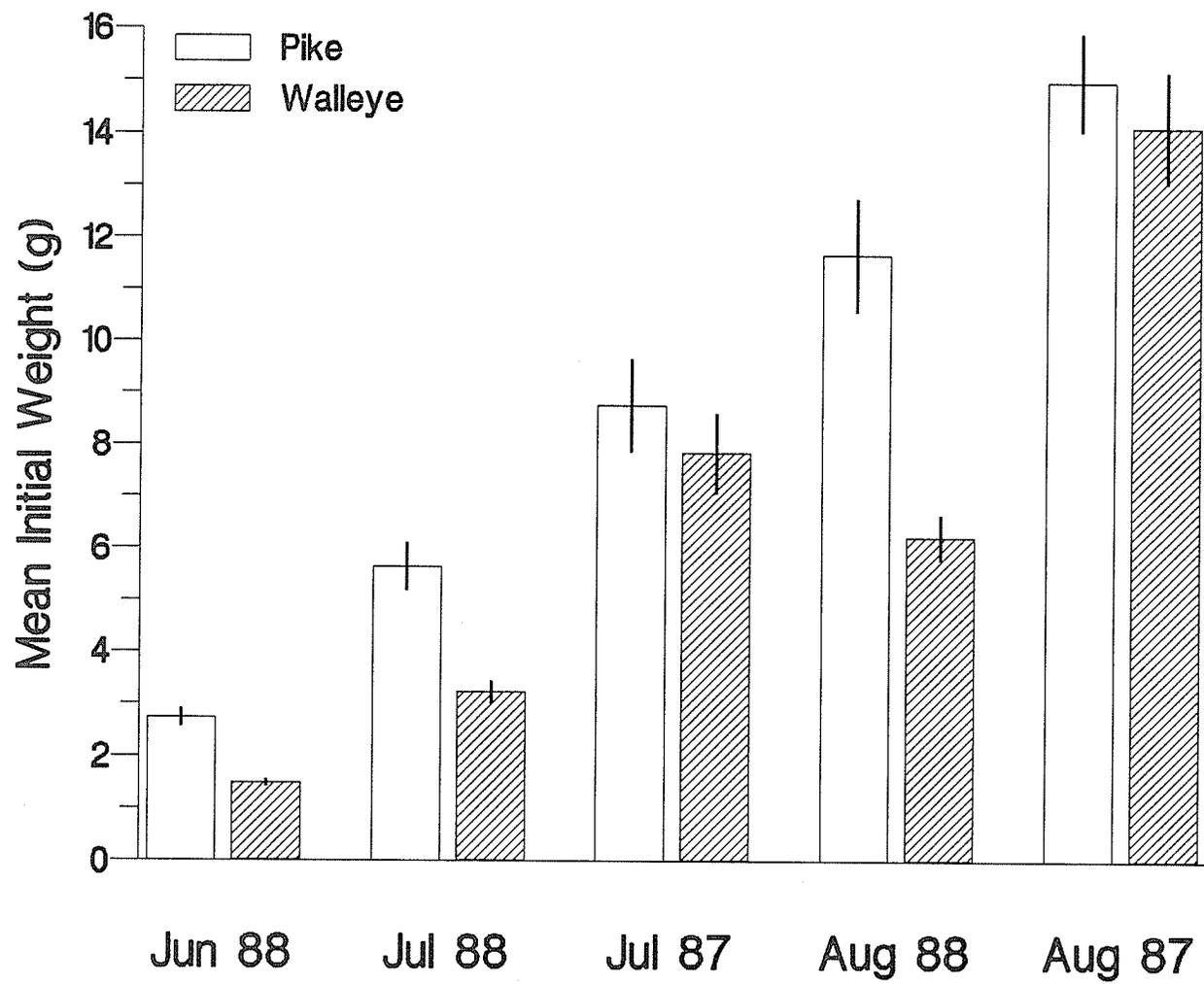
RESULTS

The results of the competition experiments changed over the course of each summer as the pike and walleye increased in size and age. For both species, mean initial weight was significantly different among all trials (ANOVA, $P < 0.0001$; Fig. 1). Therefore results will be presented with trials arranged in order of increasing size of experimental fish, rather than chronological order.

Pike weighed significantly more than walleye at the start of each trial in 1988 (t-test, $P < 0.001$), but not in 1987 ($P > 0.05$; Fig. 1). Enclosure fish biomass ($\pm 95\%$ CI) ranged from $5.63 \pm 1.48 \text{ g}\cdot\text{m}^{-2}$ in the trial using the smallest fish, to $38.82 \pm 8.80 \text{ g}\cdot\text{m}^{-2}$ for the largest fish (Table 3). This compares favourably with estimates of natural total littoral fish biomass used for similar experiments in Lake Memphremagog, Quebec (Hanson and Leggett 1985), and Lake Sövdeborg, Sweden (Persson 1987b). The range is also consistent with estimates of total littoral fish biomass in Whitefish Lake and others (Table 3). The lakes listed support coolwater to warmwater fish communities; ie. northern pike, percids and/or centrarchids are the dominant piscivores. Lake productivities range from mesotrophic (Whitefish Lake) to highly eutrophic (Lake Sövdeborg).

The mean and range of daily maximum temperatures during each experiment are given in Table 4. Mean temperatures were significantly

Ch. II, Figure 1. Mean initial weight ($g \pm 95 \% CI$) of experimental fish in each trial, with trials given in order of increasing size of fish. N=40 for each species in 1987, and n=60 in 1988.



Ch. II, Table 3. Mean and range of total enclosure biomass ($\text{g}\cdot\text{m}^{-2}$) used during each trial of the enclosure experiments, and for comparison, estimates from seine samples of total littoral fish biomass from several lakes. Trials are listed in order of increasing fish size.

Trial Date	Mean Enclosure Biomass \pm 95% CI. ($\text{g}\cdot\text{m}^{-2}$)	Range ($\text{g}\cdot\text{m}^{-2}$)
June 28 - July 12/1988	5.63 \pm 1.48 n = 15	2.20 - 10.23
July 19 - August 2/1988	11.82 \pm 3.50 n = 15	4.00 - 24.80
July 22 - July 27/1987	22.13 \pm 5.46 n = 10	12.56 - 34.23
August 9 - August 23/1988	23.85 \pm 6.13 n = 15	9.43 - 42.47
August 7 - August 17/1987	38.82 \pm 8.80	23.77 - 60.01

Location	Littoral Fish Biomass ($\text{g}\cdot\text{m}^{-2}$)	Source
L. Memphremagog Quebec	12.06 \pm 2.08 (mean \pm 95% CI)	Hanson and Leggett (1985)
Lake Opinicon Ontario	2.5 - 10.0 (range)	Keast and Harker (1977)
Lake Sövdeborg Sweden	30 - 50 (range)	Persson (1987b)
Dauphin Lake Manitoba	0.11 - 4.76 (range)	Schaap (unpubl. data)
Whitefish Lake Manitoba	7.71 \pm 1.70 (mean \pm 95% CI) 0.03 - 41.22 (range)	this study (Chapter I)

Ch. II, Table 4. Mean and range ($^{\circ}\text{C} \pm 95\% \text{ CI}$) of daily pond temperatures during five trials of the competition experiment. 1988 values are daily maxima, usually occurring at about 20:00. 1987 values were recorded daily between 16:00 and 18:00 and therefore are approximately 1 degree below actual maxima. Experimentally determined optima and range of temperatures for maximal growth of juvenile pike and walleye are also given. Ranges represent temperatures for which at least 80% of maximum growth was achieved.

Trial Date	Mean Daily Temperature ($^{\circ}\text{C} \pm 95\% \text{ CI}$)	Temperature Range ($^{\circ}\text{C}$)
July 20 - July 27 1987	25.5 \pm 0.86	24.8 - 26.9
August 7 - August 17 1987	20.1 \pm 1.29	17.3 - 22.9
June 28 - July 12 1988	23.4 \pm 0.82	21.2 - 25.8
July 19 - August 2 1988	24.6 \pm 0.66	22.9 - 26.6
August 9 - August 23 1988	21.3 \pm 0.92	18.1 - 24.1

Species	Optimal Temperature ($^{\circ}\text{C}$)	Optimal Range ($^{\circ}\text{C}$)
Pike ¹	24	20.0 - 27.5
Walleye ²	26	22.0 - 28.0

1. Bevelheimer et al. (1985).
2. Hokanson and Koenst (1986).

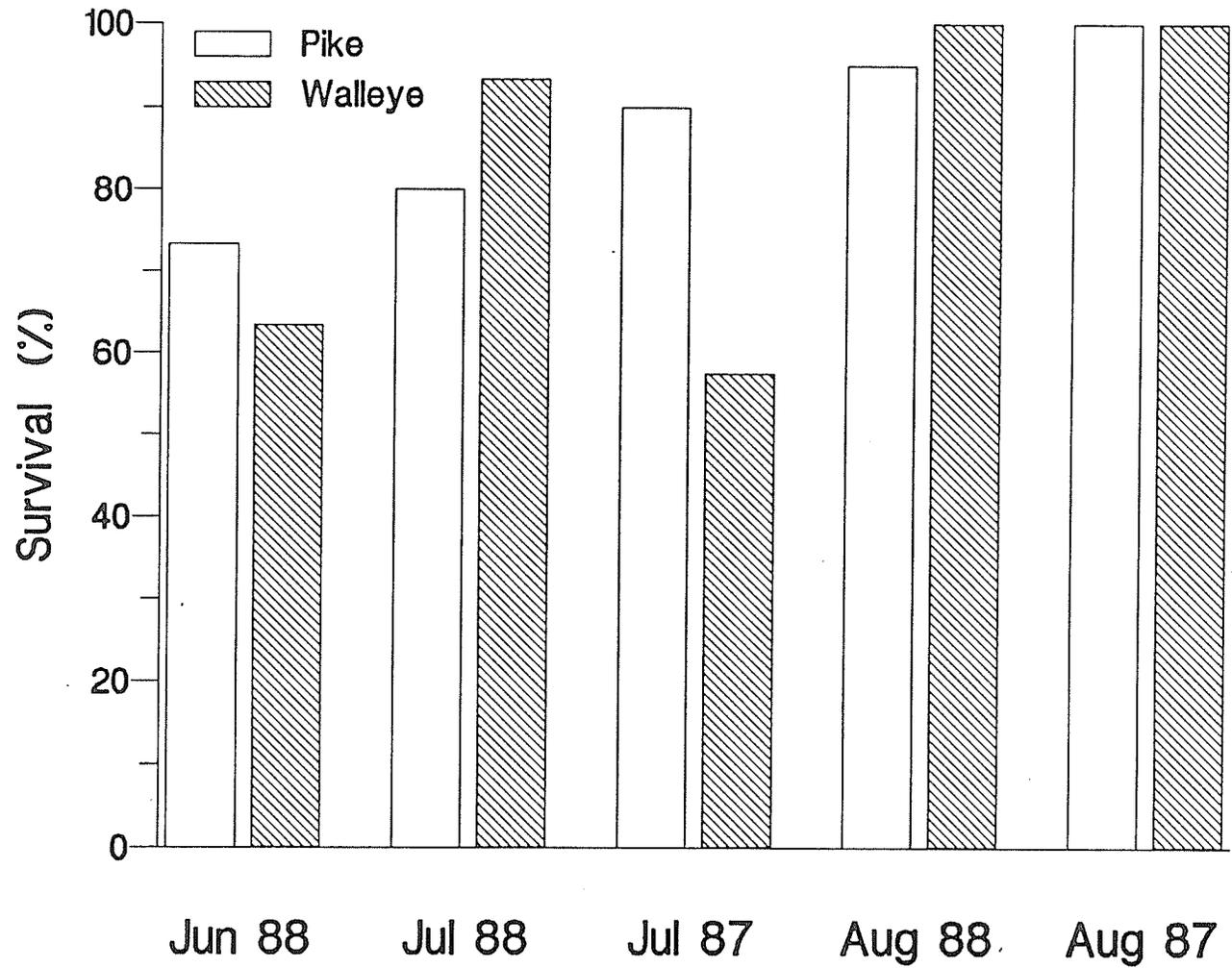
higher during the three July trials than the two in August (ANOVA and Tukey-Kramer test, $P < 0.001$). Means were not significantly different within either month. Mean July temperatures corresponded closely with those determined experimentally as growth optima for YOYs of both species (Table 4). Mean temperatures during August were lower than the optima for YOY walleye, but not pike.

Mortality

Mortality could strongly affect total enclosure production due to the small numbers of experimental fish in each enclosure. Therefore it was necessary to assume mortalities were the result of competitive interactions in order for production to be an appropriate measure of treatment effects. It was important to account for as many fish as possible in each trial so that I could assess whether this assumption was valid.

Survival was lowest in the July 1987 and 1988 trials, and was 100% in the August 1987 trial which used the largest fish (Fig. 2). Survival was not significantly different among treatments in any trial (ANOVA, $P > 0.05$). In three of the five trials pike and walleye survival (% of fish) was not significantly different (ANOVA, $P > 0.05$; Table 2) and mortalities were almost wholly accounted for. Therefore production in these trials was not biased by unexplained mortality that affected the two species unequally. However, walleye survival was significantly less than that of pike in the first trial of 1987 ($P = 0.003$). Seventeen of forty walleye (42.5 %) died compared to only four of forty pike (10 %)

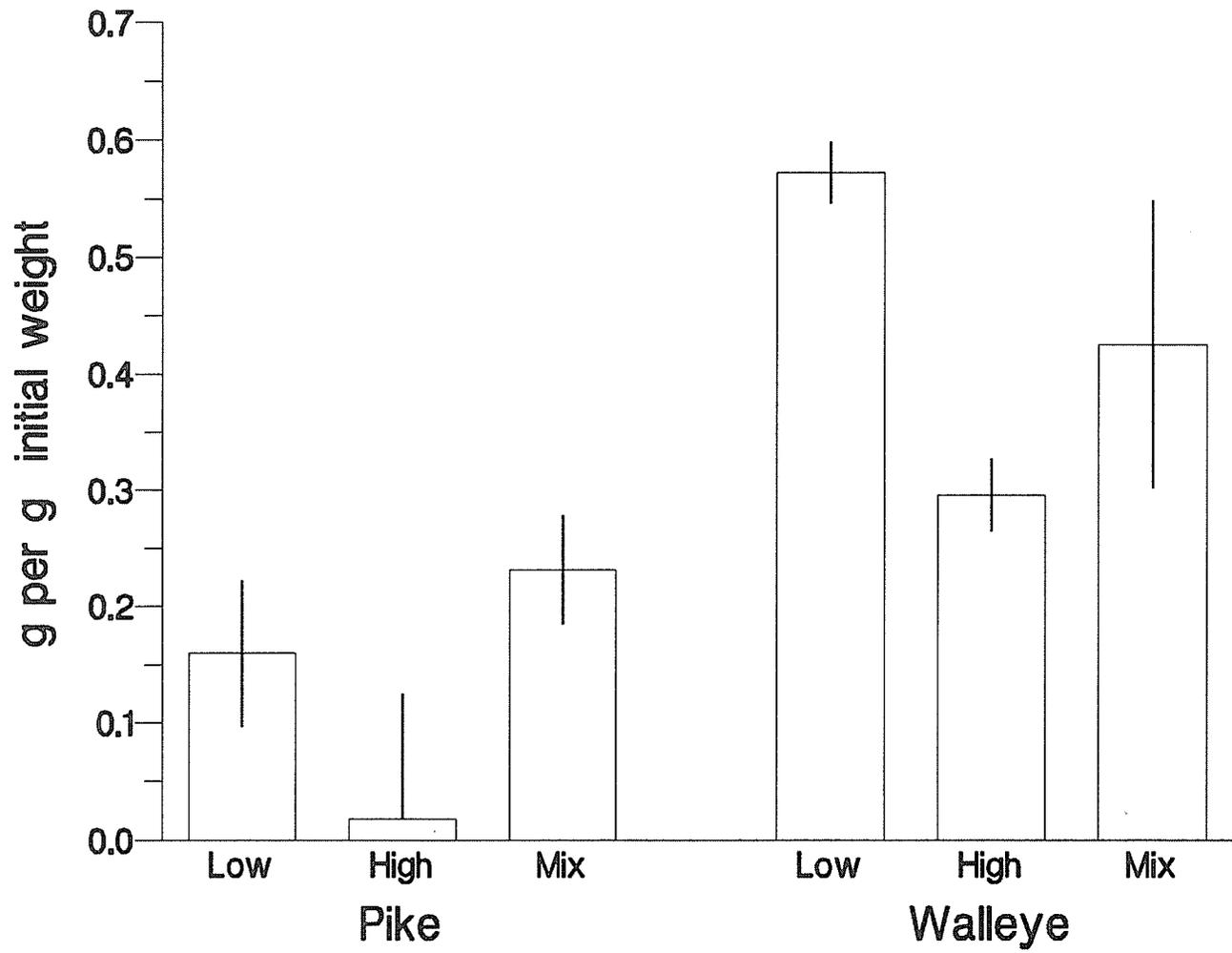
Ch. II, Figure 2. Survival (%) of pike and walleye to the end of each trial. Initial numbers of each species were 40 in 1987 and 60 in 1988. Trials are given in order of increasing size of fish.



during this trial. Of these, a total of nine walleye and one pike were removed, mostly during the latter half of the trial. These fish apparently died from starvation. All were emaciated and had empty stomachs; there were no signs of disease. I do not know whether unrecovered mortalities were predated upon or died from starvation and became hidden amongst weeds. The very warm temperatures during this trial (see Table 4) may also have been a factor in the unexplained mortalities. The assumption is however, that mortalities were caused by competitive effects on food consumption and hence condition.

In contrast, pike mortality exceeded walleye mortality threefold during the second experiment in 1988 (Table 2), making pike survival significantly less than that for walleye (ANOVA, $P = 0.04$). Ten of the twelve pike mortalities were removed within the first four days of the 14 day trial. Pike mortality was approximately equal across all treatment densities, therefore disease was perhaps a more likely cause than the food limitation occurring in some treatments. Some pike were not feeding well in the laboratory aquaria before this trial commenced. The early occurrence of mortality during the trial also implied that competition was not the cause, since competition-induced starvation should occur later during a trial, as it did in the first 1987 trial. The effect of this high mortality on pike production was quite marked (Fig. 3). This trial is excluded from further discussion of the results because it would be inappropriate to attribute treatment differences to competitive interactions.

Ch. II, Figure 3. Mean enclosure production ($\text{g}\cdot\text{g}^{-1} \pm \text{s.e.}$) for the second trial in 1988 (July 19 - August 2). When compared to walleye production, the negative effect that high mortality had on pike production is apparent.



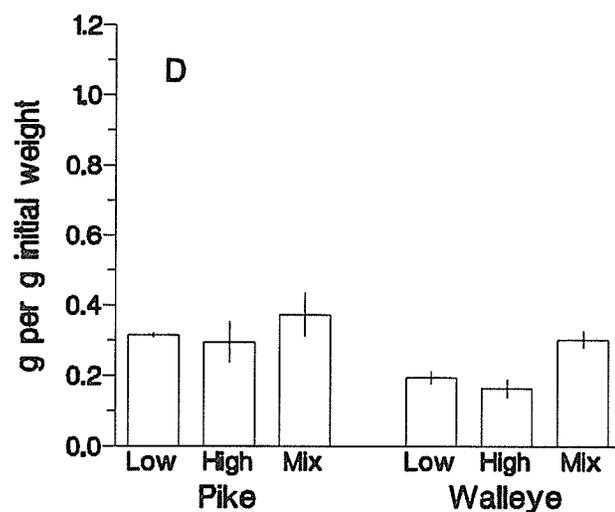
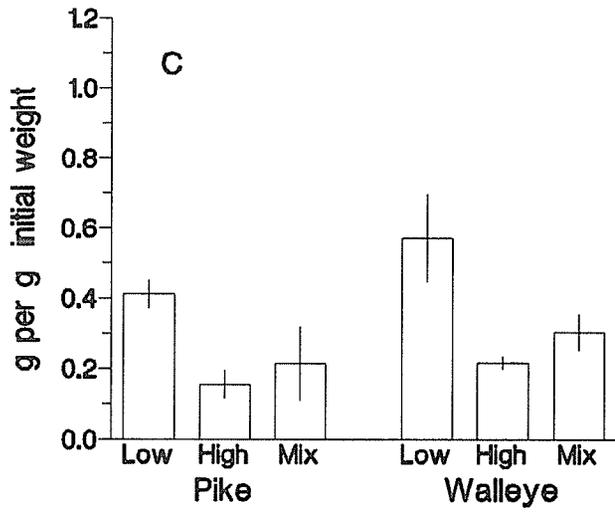
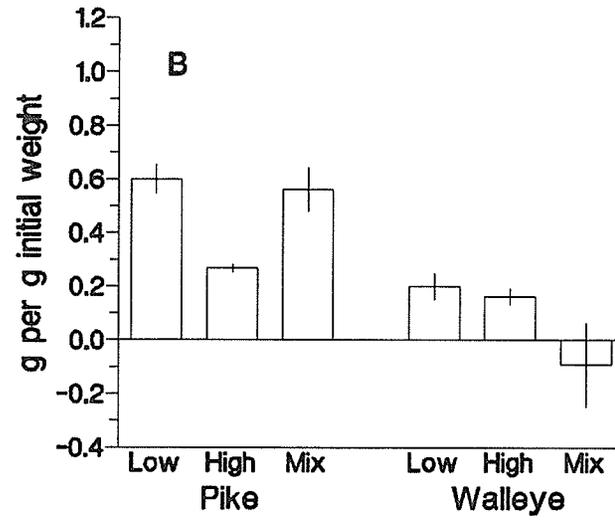
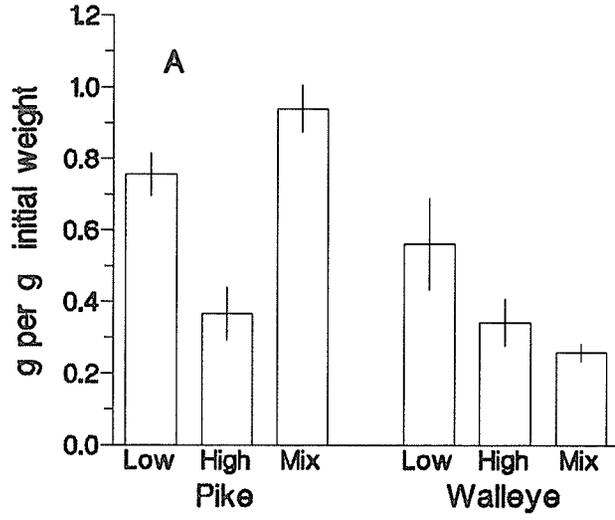
Competition

Results of the planned comparisons between treatment means are presented in Table 5. Overall, pike production was significantly higher than walleye production in the first two trials with the smallest fish, but equal in August 1987 and 1988. Total production on a per gram body weight basis declined as fish size increased in successive trials (Fig. 4).

Experimental fish in the block of enclosures with the lowest macrophyte abundance generally had slightly higher production than those in more weedy enclosures. This suggests better prey capture success when cover for forage fish was lowest, however the block effect was not significant in any trial ($P \geq 0.15$).

There was evidence that intraspecific competition occurred in all trials but the one in August 1987. Both species showed reduced production in response to addition of conspecifics (Fig. 4), although not all differences were significant (Table 5). As stated previously, this was in part due to the conservative nature of the Dunn-Sidak test. The likelihood of demonstrating a significant difference was also lessened in 1987 trials by having only two replicates per treatment. However, a highly significant trend wherein twenty-three of twenty-six high density enclosures had lower production than the low density enclosure in the same block and trial was apparent (Wilcoxon signed-ranks test for paired comparisons, $P < 0.001$). All fish gained weight in low density enclosures whereas some in high density enclosures lost weight in response to reduced per-capita forage availability.

Ch. II, Figure 4. Mean production ($\text{g}\cdot\text{g}^{-1} \pm \text{s.e.}$) in each treatment for four trials of the competition experiment. (A) June 28 - July 12, 1988; (B) July 20 - July 27, 1987; (C) August 9 - August 23, 1988; (D) August 7 - August 17, 1987. Trials are arranged in order of increasing size of the experimental fish.



Ch. II, Table 5. Results of comparisons between treatment means with the direction of differences indicated (NP = northern pike; WE = walleye; L = low density; H = high density; M = mixed species). All comparisons were tested using a significance level α' , adjusted by the Dunn-Sidak method (see text). NS = not significant; $P < 0.10$; * $P < 0.05$, ** $P < 0.01$). The results from the August 1987 trial with the largest fish are not presented here, but are given in the text (there were no significant differences for any comparison).

Trial Date	Overall	Intraspecific low vs high		Interspecific		
	NP vs WE	NP	WE	mix vs high NP	mix vs high WE	mix vs mix NP vs WE
June 28 - July 12/88	NP > WE **	L > H *	L > H (NS)	M > H **	M < H (NS)	NP > WE **
July 22 - July 29/87	NP > WE *	L > H (NS)	L > H (NS)	M > H (NS)	M < H (NS)	NP > WE *
August 9 - August 23/88	NP = WE (NS)	L > H ($P < .10$)	L > H *	M > H (NS)	M > H (NS)	NP < WE (NS)

The degree and direction of interspecific competition varied between trials. The trend was one of earlier dominance of pike over walleye and later an apparent equality of intraspecific and interspecific competition when fish were largest (Fig. 4). The response to the addition of the other species was probably dependent on the ration provided, the relative size of the predators, and each species' ability to utilize alternative food organisms when forage fish levels were reduced. Results will be outlined by presenting the outcome of each trial together with results from stomach content analyses.

June 28 - July 12, 1988

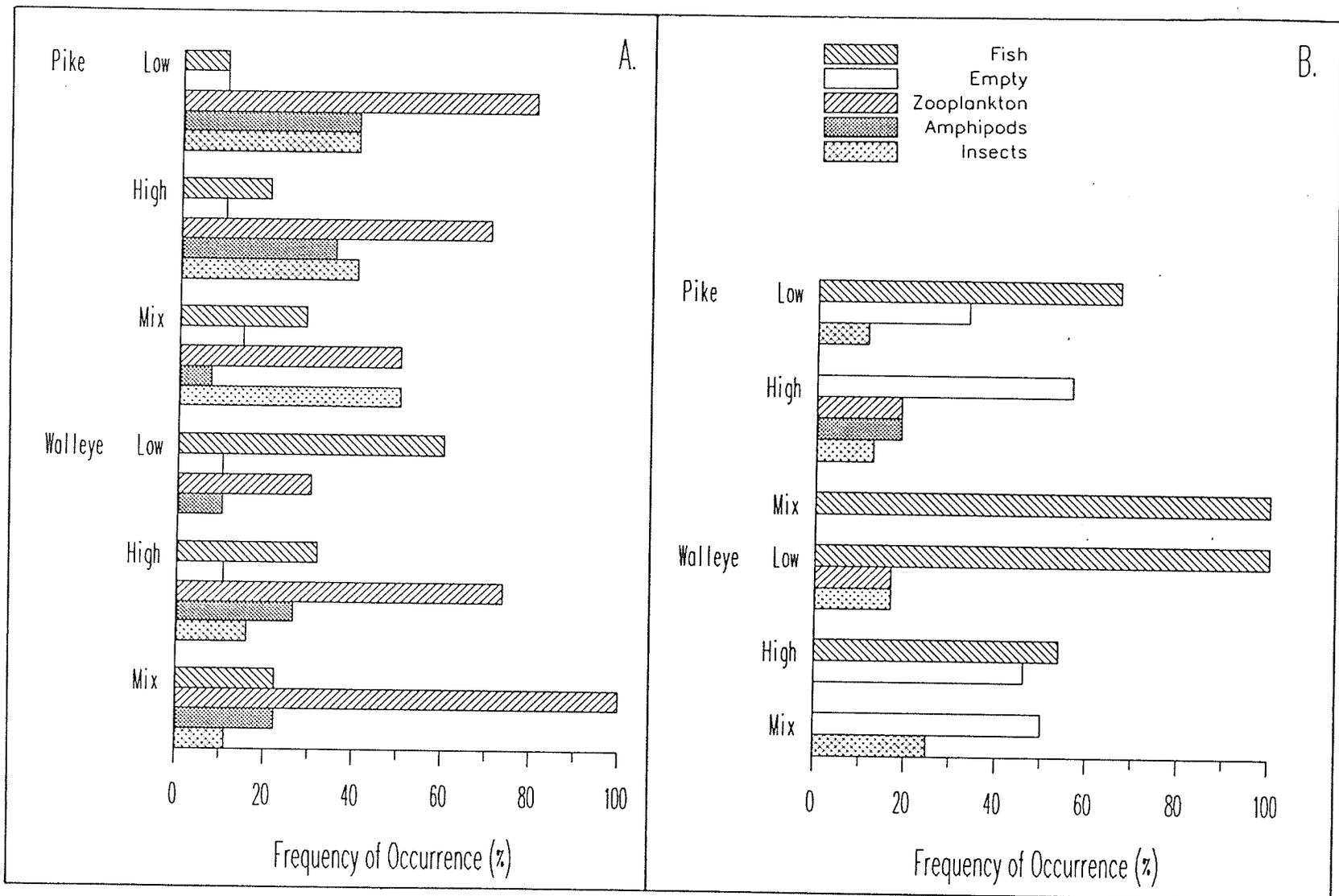
Interspecific competition favoured pike; they had significantly higher production than walleye in the mixed species enclosures (Fig. 4a; Table 5). Pike with walleye also fared significantly better than conspecifics of equivalent total numbers. This result was not accompanied by decreased production by walleye with pike compared to walleye alone at high densities. There were no differences in stomach fullness between treatments (K-W test, $P = 0.31$); reduced production in the high and mixed treatments could therefore be due to lower diet quality rather than decreased consumption. The low density walleye treatment had the highest percentage of experimental fish with forage fish in their stomachs (Fig. 5a). In the other two walleye treatments a higher percentage had consumed other food items, especially zooplankton. Zooplankters were in very high numbers when present in the stomachs and were usually not found with other food types. The similarity in food use

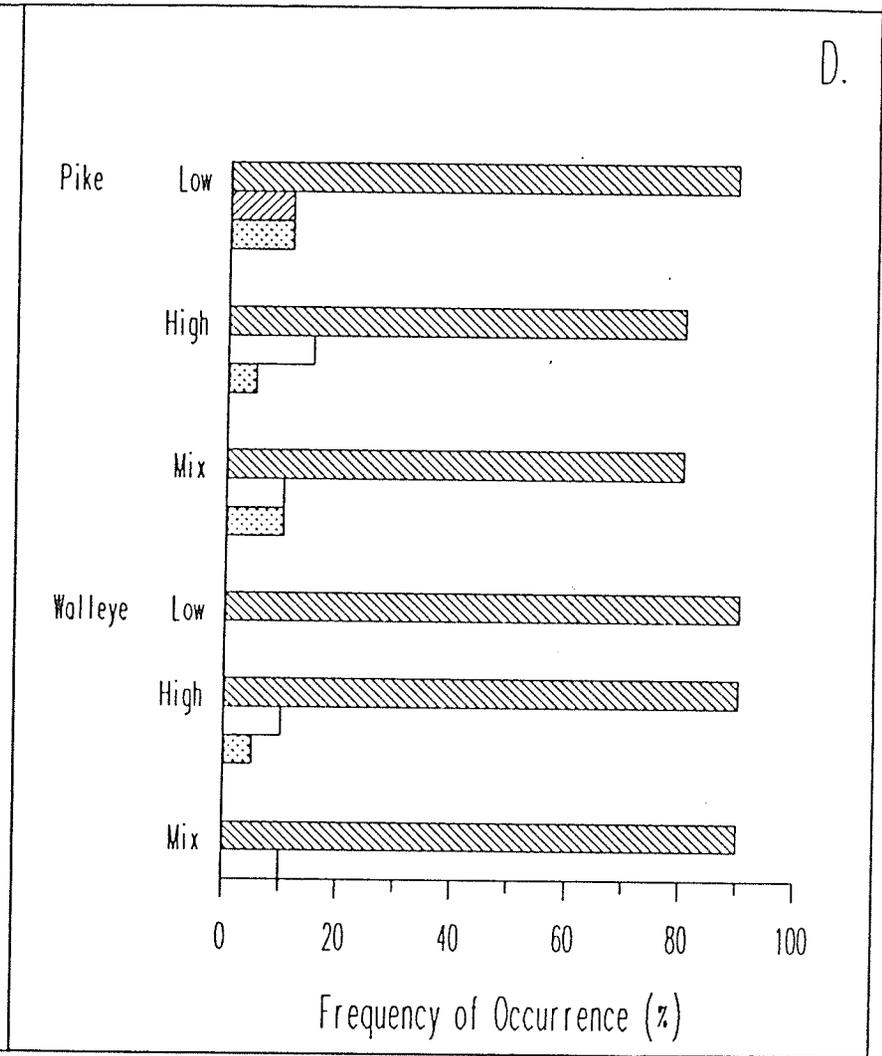
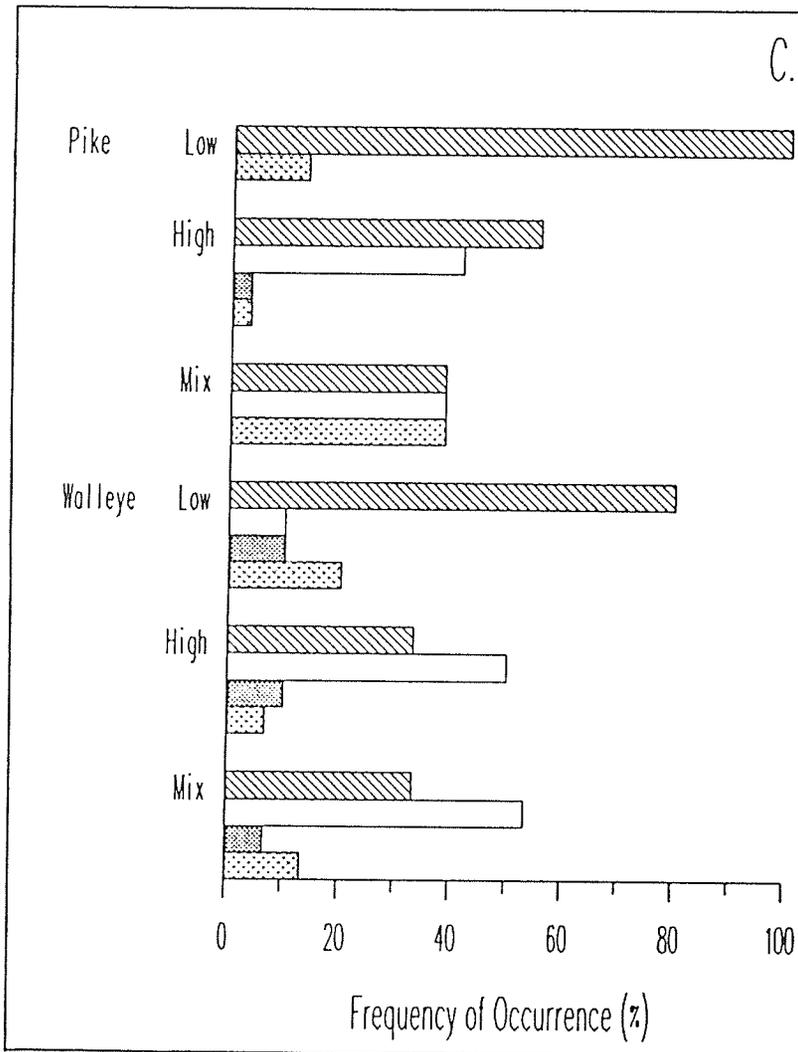
among walleye in the high and mix treatments indicates that the change in diet caused by reduced forage fish availability was no more detrimental when with five pike than when with five conspecifics. Pike in all treatment groups had a high occurrence of zooplankton in their stomachs, and again, zooplankters were usually not found with other food types. Therefore there was no evidence that pike in low density enclosures consumed more fish per capita, or that those in the mixed species enclosures obtained more forage fish than the walleye with them, yet production in these treatments was significantly higher than in the high density enclosures. This was perhaps a consequence of removing the experimental fish from enclosures one day after the last addition of forage fish. As a result, all available forage fish were probably consumed and digested the previous day.

July 22 - July 29, 1987

Experimental fish were approximately three weeks older and 50 % larger in this trial than in the one described above. Interspecific competition strongly favoured pike (Fig. 4b). Pike in mixed species enclosures had higher mean production than the pike in the high density treatment (although not significantly), and significantly higher production than the walleye with them (Table 5). Walleye production in the mixed species treatment was negative because many fish lost weight and survival was poor (40 %). Production should be highest in low density enclosures because per-capita food levels were highest, but unexpectedly, production for five walleye was no higher than that of ten

Ch. II, Figure 5. Food of experimental fish given as the frequency of occurrence of various prey categories and empty stomachs (% of fish) in each treatment group at the end of each trial. (A) June 28 - July 12, 1988; (B) July 20 - July 27, 1987; (C) August 9 - August 23, 1988; (D) August 7 - August 17, 1987. The legend for all figures is shown in (B).





(Fig. 4b). Percent survival was slightly lower in the low density enclosures however. This probably had a negative effect on production despite better mean instantaneous growth.

The pike's impact on walleye production was reflected in their diet. All pike contained forage fish, whereas the walleye stomachs were either empty or contained aquatic insects (Fig. 5b). These pike also had significantly greater stomach fullness than all other experimental groups except the walleye at low density (K-W test, $P < 0.01$). Pike and walleye in the high density enclosures had the lowest mean stomach fullness. Experimental fish in high density and mixed species enclosures typically had empty stomachs or contained forage fish (Fig. 5b). Compared to the first trial with the smallest fish, there was much less occurrence of alternative food items.

August 9 - August 23, 1988

Intraspecific and interspecific competition were equal in this trial. Both species exhibited a decrease in production when the other was added (Fig. 4c). However, the reduction was not significantly different from that caused by the addition of conspecifics (Table 5). The pattern of food use was also very similar between high density and mixed species treatments (Fig. 5c). At least 40 % of pike and walleye in both treatments had empty stomachs and fewer contained forage fish compared to fish in low density enclosures. The prevalence of other food types was low, similar to the above trial (July 1987). Stomach fullness of pike and walleye in low density enclosures was significantly higher

than all other groups (K-W test, $P < 0.01$). In the mixed species treatment fish contained less food than those in high density enclosures but differences were not significant.

August 10 - August 17, 1987

There was no evidence of intra- or interspecific competition in this trial using the largest experimental fish (Fig. 4d). None of the comparisons between treatments was significant ($p > 0.05$). Survival was 100 % in all enclosures and the majority of fish grew in length and weight. Only three walleye of twenty in high density enclosures lost weight. At least 80 % of pike and walleye in each treatment group contained forage fish (Fig. 5d). Mean stomach fullness was high and there were no differences between treatments (K-W test, $P > 0.05$). Many unconsumed forage fish were removed from all enclosures at the end of the experiment (these were usually only found in low density enclosures at the end of other trials). The ration of forage fish (25 % initial body weight per day) was therefore in excess of requirements for all treatment densities and I reduced ration levels in 1988 trials as a consequence. As will be discussed later, the lack of treatment differences in this trial is an important result.

DISCUSSION

The enclosure experiment was designed to assess the direction and intensity of intra- and interspecific competition between YOY pike and

walleye under controlled experimental conditions. The experiment itself does not evaluate the importance of competition in natural communities. Demonstrating competition in the enclosure environment does however indicate the potential results when these species interact, and the inferences that can be made about natural populations are stronger when the experimental conditions are more natural (Connell 1983; Diamond 1986). I will first discuss the degree to which the enclosures simulated the natural environment, and the appropriateness of various treatment attributes (fish density and size, food levels, etc.) before discussing the issue of competition.

Experimental Conditions

Enclosure Environment

The enclosures were located in a small pond in an effort to simulate littoral conditions. This avoided the logistical problems of establishing semi-permanent enclosures in Dauphin Lake, which is subject to strong wave action and large depth fluctuations caused by wind-driven seiches. Macrophyte abundance in the pond was similar to that found inshore in many clear lakes (eg. Whitefish Lake). The water depth in the enclosures (0.6 - 1.0 m) was also appropriate, since the abundance of littoral fish is usually greatest at similar depths (Keast and Harker 1977). One unnatural aspect of the enclosure environment was that the availability of alternate prey organisms (zooplankton and macroinvertebrates) probably declined markedly with each trial, due to

predation by fish in previous trials. The reduced opportunity to switch to alternate prey items may have intensified the negative effects of a limited prey fish supply. I did not measure the abundance of zooplankton and benthos in the enclosures, so I can not discern the degree to which this may have affected competitive interactions.

Daily water temperatures did not fluctuate more than in a large shallow lake, despite the pond's small size. Diurnal changes (the difference between the daily maximum and minimum temperature), ranged from 1.0° to 3.1° C in the pond, a smaller range than those found in Dauphin Lake, a large (522 km²), shallow, unstratified lake (Schaap 1987). Day to day changes in the pond's maximum temperature ranged from 0.0° to 2.2° C, this is comparable to the range (0° to 3° C) recorded during July and August 1985 in Dauphin Lake (Schaap 1987).

The overall range in temperature experienced by the fish generally corresponded with experimentally determined optimal temperature ranges for both species. Cooler temperatures in August partly explain the reduced production in these trials, since consumption and growth decrease at suboptimal temperatures (Elliott 1975; Bevelheimer et al. 1985; Hokanson and Koenst 1986). This was especially true for the August 1987 trial. There was no apparent food limitation at any treatment density yet production was lower than in all non food-limited treatments in other trials with equal or lower ration levels (Fig. 4).

There is no evidence that effects seen in the pond enclosures were a result of environmental factors that differ markedly from those found in natural lakes where pike and walleye coexist.

Ration Levels

Ration levels were chosen so as to provide an adequate food supply for growth in the low density enclosures, while causing food limitation in others. In the first year of the study I supplied a ration level of 25 % initial body weight per day. This level seemed appropriate for the first 1987 trial since there was evidence of food limitation in high density and mixed species enclosures. Mean temperature was close to the optimum for both species throughout the trial, so fish in low density enclosures may have achieved near maximum consumption and growth. The ration was inappropriate in the August 1987 trial however, in which no differences were found between any treatments. Cooler temperatures probably were a factor, as already discussed. Another factor was the larger size of the experimental fish. Maximum ration (consumption expressed as a proportion of body weight) and growth rate decrease as fish grow (Elliott 1975; Kitchell et al. 1977; Hurley 1986). The provided ration probably exceeded requirements at all treatment densities, and hence no treatment differences were found. Rather than being a negative result however, the lack of treatment differences demonstrated that competition does not always occur when species share a common food supply. This trial can be considered one which simulated conditions of food resource abundance.

I reduced 1988 ration levels after considering the 1987 results. Food limitation was created in high density and mixed species enclosures in all three trials, as indicated by changes in production relative to low density treatments. Cooler water temperatures and the larger size of

experimental fish again explain the reduced production in the last trial of 1988 relative to earlier trials that year.

Another aspect of the ration's suitability is the size of the forage fish. A disadvantage could be conferred on one species if its prey handling costs were significantly higher for the provided size range of forage fish (Hart and Connellan 1984). All forage fish species used in this study are natural prey of YOY pike and walleye (Hunt and Carbine 1951; Colby et al. 1979; Hart and Connellan 1984). Both species prefer forage fish that are 20 - 45 % their length; prey that are 25 - 30 % their length are considered the optimal size for growth (Beyerle and Williams 1968; Nursall 1973; Knight et al. 1984). In each trial the mean fork length of forage fish was within the preference range of both species, and prey individuals were of a wide size range (15 to 40 mm fork length). The mean fork length of pike was significantly longer than that of walleye in all trials, but the range in fork lengths always overlapped between the two species. Therefore, given these wide size ranges of competitors and forage fish in each trial, it is unlikely that one species was given an advantage by being the only one provided with an optimal size range of prey.

Enclosure Fish Density

Deciding whether enclosure fish densities were reasonable requires considering their numbers relative to available food levels. Competition experiments must manipulate densities within typical levels when enclosures are situated in the actual habitat of the species being

studied, because all resources are available at the natural levels present in the enclosures at that time (Connell 1983; Diamond 1986). In this experiment I chose levels of fish density by considering conflicting factors such as the effect of crowding if numbers were high, versus that of mortality if numbers were small. I then supplied food levels that would be more limiting in enclosures with ten fish, by providing the same total amount of food to all enclosures. I assumed this would simulate the more realistic experiment in which competitor density is manipulated within lake enclosures that contain a natural food supply. I feel I was justified in using numbers that may have exceeded natural YOY densities because food was supplied in levels appropriate to the number of pike and walleye present. In addition, total enclosure biomass in all trials was within the range of littoral fish biomass estimates found for pike-walleye lakes or other warmwater fish communities. This indicated that the enclosures were not supporting a fish biomass that exceeded what is typically found in the littoral zone of mesothermic lakes.

Another concern was whether the densities of pike or walleye made space rather than food a limiting resource, or whether crowding stressed the fish and negatively affected growth. Pike were more likely to be 'crowded' in the enclosures than walleye, a consequence of their territorial, solitary behaviour that commences during the late larval stage (Frost and Kipling 1967). Small walleye forage in shoals (Ryder 1977), and therefore the presence of 5 or 10 conspecifics probably had no negative effects on growth other than through reduced per capita food levels. Pike and walleye are cannibalistic when densities are unnatu-

rally high, both in aquaria and in the natural environment (Hunt and Carbine 1951; Frost and Kipling 1967; Chevalier 1973; Forney 1974; Swenson and Smith 1976; Giles et al. 1986), yet there was only one known instance of cannibalism (with pike) from both years of this experiment. Most mortalities were otherwise accounted for.

Lastly, enclosure fish density would have been unnaturally high if per capita food availability was reduced to a level that would rarely or never be experienced under natural conditions. This was probably not the case, since in all trials at least some fish gained weight in all high density enclosures. Evidence that food limitation does often occur among natural populations of fish, and its relationship to the potential for these species to compete, will form part of the general discussion.

I think that the experimental fish densities were appropriate then, when considered in relation to available forage fish levels and the total fish biomass usually found in the littoral habitat that the enclosures represented. The enclosure environment therefore sufficiently simulated natural conditions to allow comparison between the outcome of the experiment and the potential interactions among natural populations.

Existence of Competition

Low replication (especially in 1987) and the conservatism of the Dunn-Sidak test for comparing treatment means lowered the power of the tests and increased the probability of not detecting a real difference (ie. making a Type II error; Sokal and Rohlf 1981). Yet a number of comparisons were statistically significant, and the consistent trends

for others were in agreement with those predicted by the hypothesis of competition. For instance, the fish in low density enclosures had higher production than those in high density enclosures within the same block, almost without exception. A non-parametric test found this consistent ranking to be highly significant, therefore the trend gave strong evidence for intraspecific competition. The fact that only three of the relevant one degree of freedom comparisons testing for intraspecific competition were statistically significant is a result of the factors mentioned above, and also because differences were dependent on the relative densities of pike, walleye, and forage fish. The consistency of the trend through all trials is perhaps more important than attaching specific probabilities to differences between arbitrary treatment conditions. I do not mean to imply that parametric statistical analyses are unnecessary or superfluous to consideration of the results. I am suggesting rather, that the trends indicate consistent treatment differences which may be important to both species, especially when considering that the power of the parametric significance tests was low.

Intraspecific Competition

There was evidence of intraspecific competition for both species in three of four trials. When per capita food levels were lowered, growth and survival decreased. In the trial with the smallest fish, stomach fullness was not reduced in food limited enclosures, yet production was still lower than that in low density enclosures. The consumption of zooplankton and other invertebrates was much higher

though, indicating that diet breadth increased in response to reduced forage fish availability. Consumption of prey of less than optimal size can markedly increase foraging costs, so fish require prey of increasing size to continue growing (Kerr 1971). The conversion from an invertebrate to fish diet was demonstrated to be necessary at a small size for juvenile fish to maintain their growth, since the energy value of fish is higher than that of invertebrates (Hurley 1986). The reduced production in high density enclosures in association with increased selection of zooplankton and macroinvertebrates is consistent with the results obtained from other field experiments examining competition among freshwater fish species (Werner and Hall 1979; Clady and Luker 1982; Hanson and Leggett 1986; Persson 1987a).

In later trials, lower production and significantly reduced mean stomach fullness in high density treatments indicated that decreased forage fish availability negatively affected consumption, but not diet quality. Pike and walleye generally either contained fish or were empty; the occurrence of invertebrates was very low. Kerr (1971) developed a theoretical model that examined the relationship between growth efficiency and prey size. The model illustrated a situation in which food particles could be small enough that the energy available per item is far less than that required for its capture. Empirical evidence for this threshold minimum prey size was found by Galbraith (1967), who showed that yellow perch would not utilize prey under a certain size. This may explain why zooplankton were not consumed in later trials when the fish were at least 50 % larger than in the first. Another explana-

tion is that zooplankton were simply unavailable in later trials, as already discussed.

After a zooplanktivorous stage, benthic invertebrates become the main dietary items of YOY pike and walleye less than about 35 mm total length, but can also be important to larger juveniles and older year-classes (Hunt and Carbine 1951; Ryder and Kerr 1978; Chapman et al. 1989). The low occurrence of macroinvertebrates in the diet of fish in later trials probably reflected low availability in the enclosures, as well as reduced selection for these food types. Macroinvertebrate abundance usually decreases over the summer months in natural lakes (Hanson and Leggett 1986; Persson 1987b), due to the emergence of aquatic insect larvae and also due to predation. Predation by fish in the enclosures during previous trials may also have reduced macroinvertebrate abundance. In the last trial the forage fish ration was more than adequate and therefore macroinvertebrate availability was unimportant; almost all pike and walleye contained forage fish.

These results demonstrate the effect of density dependent food availability on growth, production and diet quality for single species assemblages. To establish intraspecific competition is an important prerequisite for the demonstration of interspecific competition (MacLean and Magnuson 1977). In this experiment the effect of adding conspecifics served as a necessary control against which the effect of adding the other species could be compared. The more interesting question to be addressed is how the experimental level of food limitation affected interactions between pike and walleye.

Interspecific Competition

The degree and direction of interspecific competition changed over the three trials during which competition occurred. Interactions were strongest in the first two trials, and pike was the dominant species. The effects of intraspecific and interspecific competition were equal in the third trial. Each trial will be discussed separately before general conclusions are drawn.

When pike and walleye were smallest, interspecific competition was strongly asymmetrical. Pike with walleye achieved significantly higher production than that of ten pike alone. The production for pike with walleye was in fact equivalent to that for five pike alone, although there was no evidence that pike in these two treatments with the highest production were capturing more forage fish or consuming more invertebrates. Production is the better indicator of competitive effects that occurred over the whole trial period than is the final day's sample of stomach contents, however. Therefore the inference is that pike probably did obtain more of the forage fish than did the walleye with them.

The large difference in pike production between high density and mixed species treatments could also in part be due to differences in foraging costs. Pike may have expended less energy obtaining the same quantity and quality of food in mixed species enclosures, due to reduced costs of territorial defence in the presence of walleye. Persson (1985) postulated that larger animals should have lower interference costs than smaller ones because of the size advantage they hold in agonistic interactions. Pike were significantly larger than walleye in this trial.

As territorial predators, they would experience interference competition for space from conspecifics. Costs associated with territorial defence should increase with conspecific density, but less so in the presence of small walleye. This advantage could explain why intraspecific competition was more detrimental for pike than interspecific interactions. Their larger size probably allowed them to gain superiority through interference and better exploit the forage fish resource. Taken together, these advantages could explain the dominance of pike over walleye in mixed species enclosures.

The other aspect of competitive asymmetry was that although pike had significantly better production with walleye than with conspecifics, the five walleye with five pike fared no worse than ten walleye. This was evidenced by the strong similarity in stomach fullness, food use and most importantly, production, for walleye in mixed species and high density enclosures. This result may also be related to the size difference between the competing species. Pike have an advantage in interference competition, as described above, but their larger size also confers an alpha (α) advantage, related to a larger species' higher feeding capacity, which causes it to remove more resources (per-capita) than smaller animals (Persson 1985). Smaller animals in turn have a K advantage, due to their lower individual food requirements. K asymmetry may reduce a larger species' feeding advantage because the smaller species' lower requirements enable it to withstand a reduction in resource availability. The K advantage may explain why walleye were not more affected by the presence of pike than conspecifics. The walleye's smaller size may however have allowed them to benefit from the availab-

ility of smaller invertebrate prey and survive the reduction in forage fish availability caused by the pike, such that production matched that of walleye in high density enclosures. The increased consumption of invertebrates brought a reduction in energy intake though, as judged by the difference in production between these fish and the walleye in the low density treatment. Feeding flexibility would perhaps enable competing fish to survive periods when preferred food of higher energetic value that maximizes growth is in limited supply. MacArthur and Pianka (1966) suggested that an individual would spend less time in a habitat when a competitor depletes the shared resource, rather than change its diet. Hanson and Leggett (1986) argue that fish in most freshwater systems may not have this option because a habitat switch would result in competition elsewhere. YOY fish may also be restricted to the littoral zone because predation pressure may be higher offshore (Werner et al. 1983; Tonn and Paszkowski 1987). Enclosures disallowed a change in habitat in this experiment, but this would be consistent perhaps with the situation faced by small pike and walleye restricted to the littoral zone of lakes. A diet shift would thus be the natural response to reduced availability of preferred food, but at the cost of poorer growth. This could affect year-class strength through two sources of mortality. Young-of-the-year fish must accumulate sufficient energy stores to escape starvation during the overwinter period (Werner 1986; Post and Evans 1989b), and smaller YOY fish are more susceptible to size dependent predation (Chevalier 1973; Craig and Kipling 1983; Werner and Gilliam 1984; Post and Evans 1989a).

In the second trial in which pike had significantly higher production than walleye, the species were equal in initial size (July 1987). The results from stomach contents analyses indicated that pike outcompeted walleye for the forage fish. The lack of a diet shift probably reflects low availability of invertebrate food in this later trial, as already discussed. Without this option the impact of pike on walleye in the mixed species treatment was especially severe; production was less than zero (Fig. 4b). This was due to higher mortality of walleye than pike (60 % versus 35 %). The high occurrence of empty stomachs suggested that food deprivation was the main cause of walleye mortality in the mixed species enclosures, although factors other than competition may have been important. Other possibilities are that very warm water temperatures during this trial (mean of 25.5° C), or agonistic interactions between walleye and territorial pike subjected the walleye in mixed species enclosures to more stress and hence higher mortality than that experienced by those in high density enclosures. The lack of alternate food items was a somewhat artificial aspect of the enclosure environment and undoubtedly played a role in the high mortality. Therefore I must conclude that the negative impact of interspecific competition on walleye, while certainly real, was stronger than what would be expected under natural conditions.

Pike with walleye had higher production than those competing intraspecifically, as in the first trial. In summary, interspecific competition favoured pike in the two trials with the smallest fish. Pike were more negatively affected by intra- than interspecific competition. Although walleye in mixed species treatments had significantly lower

production than the pike in both trials, walleye were equally affected by inter- and intraspecific competition in the first. They were more affected by interspecific competition in the second, but this was influenced by high mortality caused by artificial conditions.

In the first two trials, pike typically had higher production than walleye which were at equivalent densities and receiving the same ration (Fig. 4). This indicates that pike obtained more energy from the same food, assuming mortalities were approximately equal. The difference could result from better food conversion efficiency, an advantage possibly resulting from a lower energy expenditure for activity. Pike are "sit-and-wait" ambush predators, remaining motionless over 80 % of the time (Frost and Kipling 1967; Diana 1980), whereas walleye are active predators that forage in shoals (Ryder 1977). Mathers and Johanson (1985) stated that walleye have a lower conversion efficiency than pike, but no estimates were provided. Estimates of food conversion efficiency range from 30 - 42% for juvenile pike (Johnson 1966; Bevelheimer et al. 1983; Diana 1983), and 20 - 30% for juvenile sauger (Stizostedion canadense) and walleye (Minton and McLean 1982; Hurley 1986). These values support the suggestion that YOY walleye have a lower conversion efficiency than pike.

Intraspecific and interspecific competition had equal effects on both production and prey consumption patterns in the last trial during which competition occurred. An explanation for this outcome could again be related to the comparative α , K , and interference advantages held by each species. Pike exceeded walleye in length and weight by the greatest amount in this trial. If competition were only exploitative,

then walleye would be the predicted dominant, based on Persson's hypothesis (1985) that in the absence of interference (agonistic interactions), the smaller species' K advantage outweighs the other's α advantage when resources are limiting. Walleye production was higher than that of pike in two of three mixed species enclosures, but the difference between treatment means was not significant. The lack of dominance by either species indicated that walleye's K advantage was approximately equal to the α advantage of pike. Persson (1985) stated that the potential for a smaller competitor to be superior would increase with a decrease in resource availability. Perhaps resources were less limiting than in the earlier trials with smaller, faster growing fish that experienced warmer temperatures, and required higher rations for growth. The smaller species' advantage would also only apply as long as the larger species' prey capture efficiency, which aids its α advantage, was not markedly better. Foraging success for the two species was probably about equal since the diets of the two species were very similar, indicating that neither species outcompeted the other for the available forage fish. From this I would infer that walleye's K advantage was balanced by pike's α advantage, and also that interference was not as prevalent as in previous trials. A number of factors could explain this latter conclusion. The development of the walleye's tapetum lucidum switches their peak foraging activity from a diurnal to crepuscular or nocturnal habit in clear water (Ryder 1977). The tapetum lucidum starts to develop when walleye are about 30 mm total length (Bulkowski and Meade 1983); the switch from positive to negative phototaxis is essentially complete at fork lengths of about 70 mm

(Braekevelt et al. 1989). My observations during the experiment were in agreement with the latter observation; walleye negative phototaxis was most evident in the two August trials with the largest fish. Walleye were usually observed resting on the bottom amongst vegetation during daylight hours and were more difficult to locate than pike which could be found at all depths. Assuming walleye were predominantly inactive in the day once negatively phototactic, they would not be as subject to territorial aggression from the diurnal pike. Perhaps this temporal separation reduced interspecific interactions in later trials, although it would not reduce exploitative competition since the food resource was still being shared.

Conclusions

The field experiment demonstrated competitive interactions under the given enclosure conditions. An important question is whether the experimental results can be extrapolated to natural populations. Additional information was used to help judge how closely environmental conditions, prey availability, and competitor density and size used in the experiment matched those found in natural communities (Connell 1983; Diamond 1986). Competitive interactions were strongest in this experiment when there was the greatest similarity in activity pattern, food use, and body size. Competition was not demonstrated when the food supply was not limiting. Presumably these findings would also be true for YOY pike and walleye in the natural environment. The implications for natural populations of YOY pike and walleye that can be derived from

my results will be further discussed when I integrate the findings from all chapters in the concluding general discussion.

This study illustrated that manipulative field experiments are a useful means by which to examine competitive interactions. A more complex experimental design would be required however, to compare the relative importance of competition, predation, and environmental factors in determining the relative abundance of these two species. Such large scale experiments have been conducted with amphibian species (DeBenedictis 1974; Wilbur 1987), and marine plant-herbivore and intertidal invertebrate communities (Connell 1975; Lubchenco 1986), but I do not know of any examples for freshwater fish. No doubt this is a consequence of the high cost and labour intensive nature of conducting large scale enclosure experiments. This experiment was also restricted by testing for competition under only a limited set of conditions. It would be profitable to repeat the experiment under different conditions such as higher, lower, and unequal competitor densities, different forage availability, and different water clarities. The biological mechanisms determining competitive dominance would presumably differ in importance with these changes. Another improvement would be to conduct an enclosure experiment in situ, creating larger more natural mesocosms that would more closely represent typical food levels and environmental conditions experienced by natural populations. This would also remove any unnatural effects caused by my providing prey fish only once a day.

The results of this experiment are important, despite its limitations, because they demonstrate that YOY pike and walleye will compete under semi-natural conditions. Competition between these species has

often been inferred (eg. Scott and Crossman 1973; Forney 1977; Craig and Smiley 1986) but never directly tested by manipulative field experiments. I think that this study improves on previous field experiments that tested for competition between freshwater fish species which suffered from poor design or lack of proper replication. True replication in this experiment ensured that the outcome was the consequence of real treatment effects and not other uncontrolled factors that can result if treatments are not placed together in space and time. This made the results more conclusive than those derived from experiments that do not replicate or only pseudoreplicate the treatments (Connell 1983; Hurlbert 1984; Diamond 1986).

The complexity of the natural environment makes competition difficult to detect. Field experiments are a valuable tool for examining competition because they control other contributing factors and allow the interactions of interest to be examined, but they do not determine the processes behind the observed effects. The influences of competitor density, prey availability, and space were difficult to distinguish in this experiment. My suggested explanations for each trial's outcome must therefore be considered speculative because the real mechanisms behind each result cannot be ascertained by this field experiment alone. By searching for mechanisms that determine competitive dominance, a better understanding of pike-walleye interactions can be achieved. One possible influence on relative foraging success and hence competitive superiority, that of water clarity and light availability, will be examined in the following chapter.

CHAPTER III:

**The effect of turbidity on young-of-the-year
northern pike and walleye feeding success**

INTRODUCTION

Individuals that can best exploit a limited food resource should have higher growth rates, all else being equal. There should be strong selective pressure for young-of-the-year (YOY) fish to maximize absolute growth rate or surplus energy during their first summer because this strategy would maximize the probability of escaping size dependent starvation and predation (Werner 1986; Post and Evans 1989a; 1989b). Differential foraging ability, through its effect on growth and survival, is therefore a primary mechanism by which competitive dominance of a species may be determined (Hanson and Leggett 1986; Werner 1986; Persson 1987b). Competitive dominance for any one species is not usually fixed however, but rather is dependent on the environmental conditions which influence the relative foraging abilities of interacting species.

Light is one of the critical components of the abiotic environment that affects feeding in fish. Kerr (1971) used a model incorporating prey search to show that the growth efficiency of a predatory fish is influenced by its visual detection limits. Decreased prey visibility can decrease growth efficiency substantially, especially when prey are scarce and competition is most likely to occur. YOY northern pike and walleye are potential competitors that coexist in clear and turbid waters, but the light levels for foraging to which each is best adapted are dissimilar. Therefore differences in relative foraging ability form a potential mechanism by which the species that is best adapted to the

ambient conditions of light availability may gain a competitive advantage.

Walleye undergo a switch from positive to negative phototaxis as the tapetum lucidum develops during the juvenile period. The tapetum is a reflective layer in the retina that improves visual sensitivity by increasing the proportion of incoming photons of light that stimulate the retinal cells. It is an adaptation for vision in environments of low light availability (Nicol et al. 1973). Moore (1944) was the first to describe the structure of the walleye tapetum and relate its function to the often turbid conditions of the walleye's environment. Walleye feed primarily at twilight or even at night in clear water but are also well adapted to forage diurnally when light is limited by turbidity (Ryder 1977). The tapetum lucidum is essentially fully formed when juvenile walleye are about 125 - 140 mm fork length (Braekevelt et al. 1989). Functionally however, the visual sensitivity gained by gradual changes in both the rod cells and the tapetum of the retina is almost totally complete at about 70 mm fork length (Braekevelt et al. 1989).

In contrast, pike do not undergo this developmental change and are adapted for high visual acuity in clear waters (Ali and Klyne 1985). The eye of pike has a "yellow cornea", an intraocular filter which increases the contrast of objects viewed against background illumination. While useful in clear water, it does not have this effect in turbid conditions (Ali and Klyne 1985). The lateral line monitors water displacements and probably aids detection of nearby prey when vision is limited by low light availability (Frost and Kipling 1967). Sensory input from the lateral line is at an optimum when the body is held

motionless, hence the pike's elongate body form and "sit-and-wait" ambush style of predation make the pike's lateral line an important means by which it can detect prey (Lythgoe 1978). This sedentary style of predation is also one adaptation that contributes to their relatively high growth efficiency, since little energy is used in searching for prey. Pike probably forage diurnally in turbid conditions to take advantage of maximum light availability, but their growth may be reduced under such conditions, due to higher energetic costs for foraging. As Kerr (1971) suggested, decreased prey detection limits may require fish to search more actively for prey, thus decreasing growth efficiency. Vollestad et al. (1986) noted that this mechanism was a possible explanation why pike had poorer growth in a turbid river than in a less turbid lake, despite higher prey availability in the turbid habitat. In Dauphin Lake, Manitoba, adult pike exhibit a dramatic increase in food consumption and growth when the water becomes clear immediately following ice formation, evidence that their feeding may be visually limited during the turbid open-water season (Craig and Babaluk 1989). This study also found a positive correlation between summer condition of pike and secchi depth, based on data from 37 lakes in central Canada. No such relationship was demonstrated for the walleye in the same lakes.

Based on these interspecific differences in visually optimal conditions for foraging, my hypothesis is that YOY pike and walleye should each have an opportunity for a competitive advantage over the other species, competitive superiority being influenced by the visual conditions for prey capture. The purpose of this study is to test the hypothesis that relative foraging success of YOY pike and walleye

changes under different experimental conditions of ambient light level and turbidity. The main prediction is that pike should have better foraging success than walleye in clear conditions, and walleye should have the advantage in turbid waters once the tapetum has developed. Both species should be able to capture prey effectively in clear waters before this time. The influence of tapetum development will be examined by comparing walleye foraging success among trials conducted at different times over the early juvenile period. The prediction is that foraging success for walleye in clear conditions should decline in successive trials, and improve in turbid treatments. Furthermore, evening light levels should provide more favourable conditions than daylight levels for negatively phototactic walleye in clear water.

MATERIALS AND METHODS

Experimental Design

The experiment was designed to examine the effects of two levels of both turbidity and ambient light on pike and walleye foraging success. Feeding in turbid water was compared to that in non-turbid conditions. Ambient light was maintained at daylight and dusk levels. Pike and walleye were held in separate aquaria, so the experiment examined three factors at two levels each (two light levels x two turbidities x two species). The experiment was split in time with trials in the early afternoon (12:00-14:30) and evening (19:00-21:30) in order that fish fed at an appropriate time of day for each light

level. Eight aquaria were available, so the four treatment combinations (two species x two water clarities) were replicated within each time period. Since day and dusk treatments were separated in time, each represented a block to the other two factors, making the experiment a split plot design rather than a 2 x 2 x 2 factorial. The layout of the experiment thus used light levels (ie. time of day) as main "plots", within which the four turbidity x species combinations were randomly assigned to the eight "subplots". The experiment was repeated over two days to increase sample size. It should not be assumed that experimental conditions were homogeneous between days, therefore it was appropriate that each day represent a block (Sokal and Rohlf 1981). Block and treatment effects were considered fixed (Model I); the complete design is illustrated in Fig. 1.

A split plot layout was used because a greater difference between levels of the main treatment (ie. day and evening) than between those of sub-factors was expected with this design. Greater precision is achieved for measuring differences between subunit levels because less precision is required for comparing main treatment effects. Main treatment effects were tested against a main plot error term. An important assumption is that main plot error will be larger than subunit error, except by chance (Steel and Torrie 1980). If this is not the case, responses to the different main plots were more alike than those to different subunits. If the main factor effect (light level) is not significant in this situation, the model can be reduced to a blocked two species x two water clarities factorial design, with day and evening observations pooled to become (pseudo) replicates of the remaining treatment

Ch. III, Figure 1. Split plot design for the feeding experiments, with whole units in a complete block arrangement. Blocks are the two consecutive days on which the experiment was conducted for each trial. Ambient light levels (day and evening) formed the two main plots within each block. The four species x water clarity combinations were randomly assigned to the eight subunits within each main plot, as represented by the aquarium numbers.

DAY 1

	PIKE	WALLEYE
CLEAR	1	2
	5	3
TURBID	4	8
	6	7

DAY 2

	PIKE	WALLEYE
CLEAR	4	7
	6	5
TURBID	3	1
	2	8

DAY

	PIKE	WALLEYE
CLEAR	2	3
	8	4
TURBID	7	1
	6	5

	PIKE	WALLEYE
CLEAR	4	1
	5	6
TURBID	3	2
	8	7

EVENING

combinations. This increases the error degrees of freedom and improves the precision of species and water clarity comparisons that is lost by using a split plot design when responses to different light levels are unexpectedly similar.

An assumption of any blocked design is that block effects do not interact with treatments (Sokal and Rohlf 1981). In this experiment it was assumed that responses for any light level, species or water clarity did not depend on the day, so that block x subunit effects could be included in the subunit error term. Subunits contain observations on more than one experimental unit so a measure of pure error (variation amongst units treated alike) is available for testing this assumption of no interaction. The analysis of species and water clarity effects thus depends on whether block x subunit interactions are significant. If they are, subunit simple effects must be examined within each block (day), otherwise subunit effects can be tested against a subunit error term that incorporates the negligible sums of squares due to interaction (Steel and Torrie 1980).

Procedure

The experiment was performed on three occasions at three week intervals during July - August 1988, in the laboratory of the Methley Beach Walleye Rehabilitation and Research Station near Dauphin Lake, Manitoba (Chapter I, Fig. 1). Pike were collected by seining along a weedy bank of the Turtle River, approximately 2 km upstream from where it flows into Dauphin Lake. I collected walleye in trap nets set in the

rearing ponds at the Research Station. Fathead minnows (Pimephales promelas) were collected from two small ponds at the same location and used as forage fish in all trials. In the second trial, spottail shiners (Notropis hudsonius) captured in the littoral zone of Dauphin Lake were also used, as I was unable to obtain sufficient numbers of fathead minnows. All pike and walleye were collected at least three days before a trial and held in 120 l aquaria. The fish of both species were separated into two groups, with enough in each group for each day of the two day trial. Fish in each group were fed ad libitum until the evening before the day they would be used in the experiment. They were then deprived of food until the experimental feeding period. Duration of food deprivation varied somewhat between the two days of each trial because forage fish were not removed at the same time each evening. This was one reason for making the day of an experiment a block effect.

In the first and second trial four pike or walleye were introduced into each aquarium. Forty fathead minnows per aquarium were provided in the first trial. Fifty forage fish (35 fathead minnows and 15 spottail shiners) were provided in the second trial. The number was increased because of the larger size of the experimental fish. Three experimental fish were used in each tank during the third trial. Forty fathead minnows were provided to each aquarium in this last trial. Experimental and forage fish were always assigned randomly to the aquaria. ANOVA was used to test whether mean experimental fish sizes (fork length and weight) were the same for all tanks within each trial. This was largely the case; in only one run of four, and only in the second trial were pike from different aquaria significantly different in

fork length and weight (ANOVA, $p < 0.05$). This supports the claim that fish were assigned randomly to the tanks.

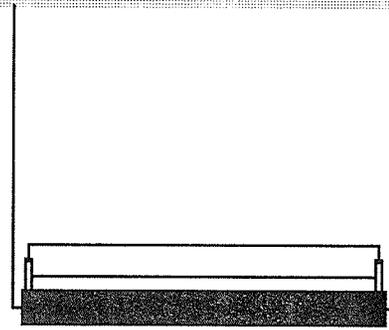
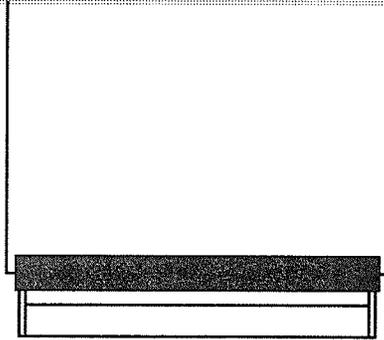
All treatment combinations were represented by at least one aquarium, but the number of true replicates was decreased from two to one aquaria during day and evening runs on the second day of the first trial, and also during the second evening run in the second trial. This was a result of not having sufficient numbers of pike and walleye to complete the full experiment. Trials one and two were analyzed accordingly as unbalanced designs, using least squares estimates for all comparisons of treatment means (Steel and Torrie 1980; SAS Institute Inc. 1985). In contrast, the last trial was a balanced design with equal replication of all treatment combinations.

All aquaria (60 x 60 x 40 cm) were filled to a volume of 100 l with water from the rearing ponds, filtered through 44 μm NitexTM mesh. Water temperature for all trials was 20 ± 0.5 °C. The sides of each aquarium were covered with sheets of translucent green plastic to limit light transmission between adjacent aquaria. Single 15 W natural spectrum fluorescent bulbs (45 cm long) in standard fixtures were suspended 25 cm above the water surface and centred over each aquarium (Fig. 2). This produced 20 - 30 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ of illumination at the water surface for daylight trials, as measured by a Li-Cor^R quantum sensor (Model LI-185). This level was below the range of local mid-afternoon light intensities recorded on overcast days (100 - 300 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$). Simulating midsummer daylight conditions (100 - 2000 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ recorded locally outside) was not possible due to the constraints of the available lighting system. Evening light intensities were produced by

Ch. III, Figure 2. Lighting arrangement for the feeding experiment. A). Daylight levels were produced by hanging one natural spectrum 15 W bulb 25 cm above each aquarium. B). Evening levels were simulated by inverting the bulb fixtures so that they formed a shield blocking direct downward rays from each bulb.



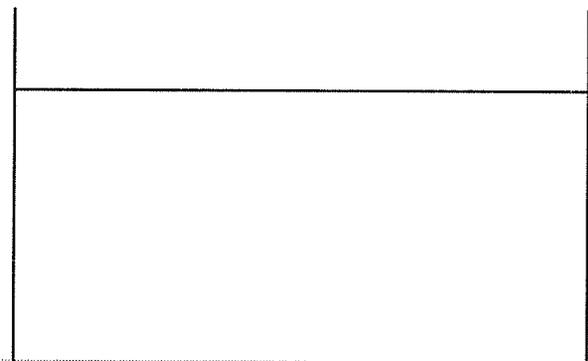
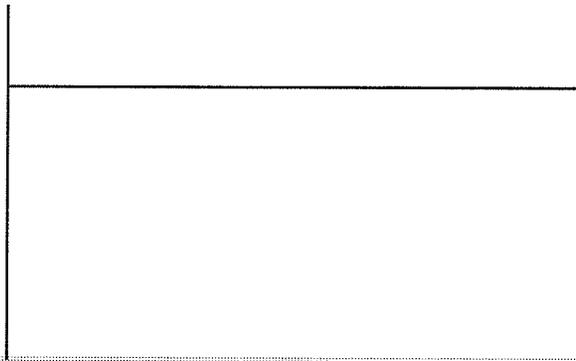
light fixture
bulb



123

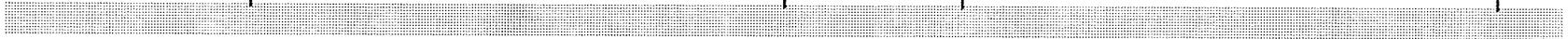
water
surface

100 l
aquaria



A. DAY

B. EVENING



inverting the bulb and fixture so that direct light was prevented from reaching the water surface (Fig. 2). This reduced light intensities to 1.0 - 3.0 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at the water surface, which compared well with outdoor levels measured around sunset (0.35 - 10.0 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$).

Preliminary experimentation, using varied periods of mixing and settling for different amounts of clay, were conducted to develop a protocol that would give a consistent turbidity level of 60 - 80 NTU (Nephelometric Turbidity Units) for all trials. I used a fine light brown clay called kaolin, a clay mineral derived from weathering of rock minerals such as feldspar (Gary et al. 1974). Kaolin is present in lake sediments in large prairie lakes such as Lake Winnipeg (Kushnir 1971). The kaolin had been sieved to include only clay and silt sized particles (< 4 μm and 4 - 60 μm , respectively). It is this silt-clay fraction of lake sediments that currents constantly mix into the water column to create turbid conditions (Kushnir 1971).

For each tank receiving the turbid treatment the following procedure was used. Forty grams of clay were added to 750 ml of water and stirred thoroughly until no dry clay remained. This slurry was poured into each of the appropriate aquaria. Air was bubbled vigorously through an airstone on the bottom of all tanks to achieve maximum suspension of the added clay in the turbid aquaria and to ensure that the water in all aquaria was well oxygenated. A 50 ml water sample for turbidity determination was then collected just below the surface in each aquarium. Samples were collected in clear and turbid water to make the degree of disturbance after fish were introduced equal for all groups. Another sample was collected after a 30 minute period of

aeration and mixing. Mesh screens were installed at this time to partition aquaria into separate sections for the experimental and forage fish. The airstones were removed before fish were introduced so that normal feeding behaviour would not be disrupted by the forage fish orientating around rising bubbles or into the currents created by them. Water samples for turbidity were again taken following these steps, then the aquaria were left undisturbed for one hour. During this time an initial settling of suspended clay occurred and the fish were given a period of recovery after being transferred into the aquaria. The hour provided sufficient time after the air supply was removed for the initially rapid settling of the clay to slow down before feeding commenced. In this way the turbidity level changed very little during the feeding period. At the end of the hour, water samples were collected both before and after the screens were removed. The feeding period then commenced and lasted one hour. This was considered a suitable length of time for fish to feed without allowing all to become satiated or to reduce forage numbers to levels that would affect foraging success. A final water sample was taken just before all fish were removed from each tank. Standard methods (APHA 1985) were used to determine NTU with an HF Instruments Model DRT-15 Turbidimeter. Although samples were collected in all aquaria, turbidity at each step was determined for only one of the non-turbid aquaria, and for all turbid aquaria. I had determined during preliminary experiments that there was little variability in NTU among non-turbid samples.

At the end of each feeding trial all fish were removed from each tank and killed in a strong solution of MS-222 anaesthetic. The body

cavity of each pike and walleye was cut open and the gastrointestinal tract rinsed with 5 % formalin solution to preserve stomach contents. On each day the fresh fork lengths (to nearest 0.5 mm) and blotted wet weights (to nearest 0.001 g using a Mettler AE 300 balance) of unconsumed forage fish from one aquarium were measured before freezing. All unconsumed forage fish and the pike and walleye were then frozen whole for later analysis.

Analyses

McIntyre and Ward (1986) showed that fathead minnow fork length could be estimated from a highly significant linear relationship between this measure and the "GAP" length of the left pharyngeal arch (the length between dorsal and ventral extremities of the pharyngeal arch). Pharyngeal arches are distinctive for many shiner and minnow species (Scott and Crossman 1973), and are persistent in the gut of predators. Therefore they are useful for species identification and size estimation of consumed forage fish. To estimate the length and weight of forage fish ingested by pike and walleye, relationships between these variables and the length of the left pharyngeal arch were determined for each species of forage fish in the following manner. Forage fish were thawed after approximately equal periods of preservation, in order that body shrinkage due to freezing could be assumed equal for all groups. Differences were probably negligible considering that over 85 % of body shrinkage occurs during the first day of preservation (Glenn and Mathias 1987). One pharyngeal arch was removed from those fish which had their

fork lengths and wet weights measured immediately after the end of a trial, before they were frozen. The GAP length of the arch was measured using 40X magnification under a dissecting microscope with a calibrated ocular micrometer and then converted to actual mm. Least squares regression was used to determine linear relationships for fresh fork length versus preserved GAP and the natural log (\ln) of fresh wet weight versus $\ln(\text{GAP})$ for each forage species. Other fathead minnows and spottail shiners which had been measured and then frozen during the summer were treated in the same manner and the data included in these regressions. When equal preservation was not possible, separate regressions were constructed for each preservation group and compared by ANCOVA. Data were pooled if there were no significant differences in slope and intercept. Pharyngeal arches were removed and measured for all other unconsumed forage fish, and their fresh fork lengths and weights were estimated from the established regression equations.

Pike and walleye were also thawed after equivalent periods of time following each trial. The thawed fork length (to nearest mm) and wet weight (to nearest 0.1 g) of each pike and walleye were measured. The number of consumed forage fish of each species was also recorded, and stomach fullness was assessed on a scale from 0 to 3 (0 = empty to $\frac{1}{4}$ full; 1 = $\frac{1}{4}$ to $\frac{1}{2}$ full; 2 = $\frac{1}{2}$ to $\frac{3}{4}$ full; 3 = $\frac{3}{4}$ to full). Lastly, the GAP length of one pharyngeal arch from each ingested forage fish was measured, following the same procedure as used for the unconsumed forage fish. Fresh fork lengths and weights of each were then estimated from the appropriate regression equations.

Comparisons between treatments required a measurement that represented overall foraging success in each aquarium. Two measures were devised; the first was the weight of consumed forage fish, standardized by expressing consumption on a per g body weight basis. This was done because pike presumably had a larger absolute stomach capacity by being larger than the walleye in all trials. The fresh weight (g) of each ingested forage fish was estimated from GAP versus weight regression equations, then the total weight (g) of forage eaten per g fish was calculated for each tank. This value better represents the size of a meal than does numbers consumed, since forage fish were of a broad range in weight. For the second measure, stomach fullness values were averaged for each aquarium. The stomach fullness index, although subjective, is automatically standardized for differences in stomach capacity and therefore is a good measure of the relative degree of satiation, assuming that satiation is represented by a full stomach. Data from each trial were analyzed by ANOVA. The split plot model was reduced to a blocked 2 x 2 factorial when appropriate, following the criteria already outlined in the description of experimental design. Only pre-planned comparisons of treatment means were made, to minimize the probability of making a Type I error. The comparisons were: clear versus turbid for each species, and walleye versus pike within each water clarity. These simple effects were examined within each light level only if this latter factor showed significant interaction with the other treatments. All statistical analyses were made using SAS statistical packages (see Appendix IV for SAS Model statements).

RESULTS

Turbidity

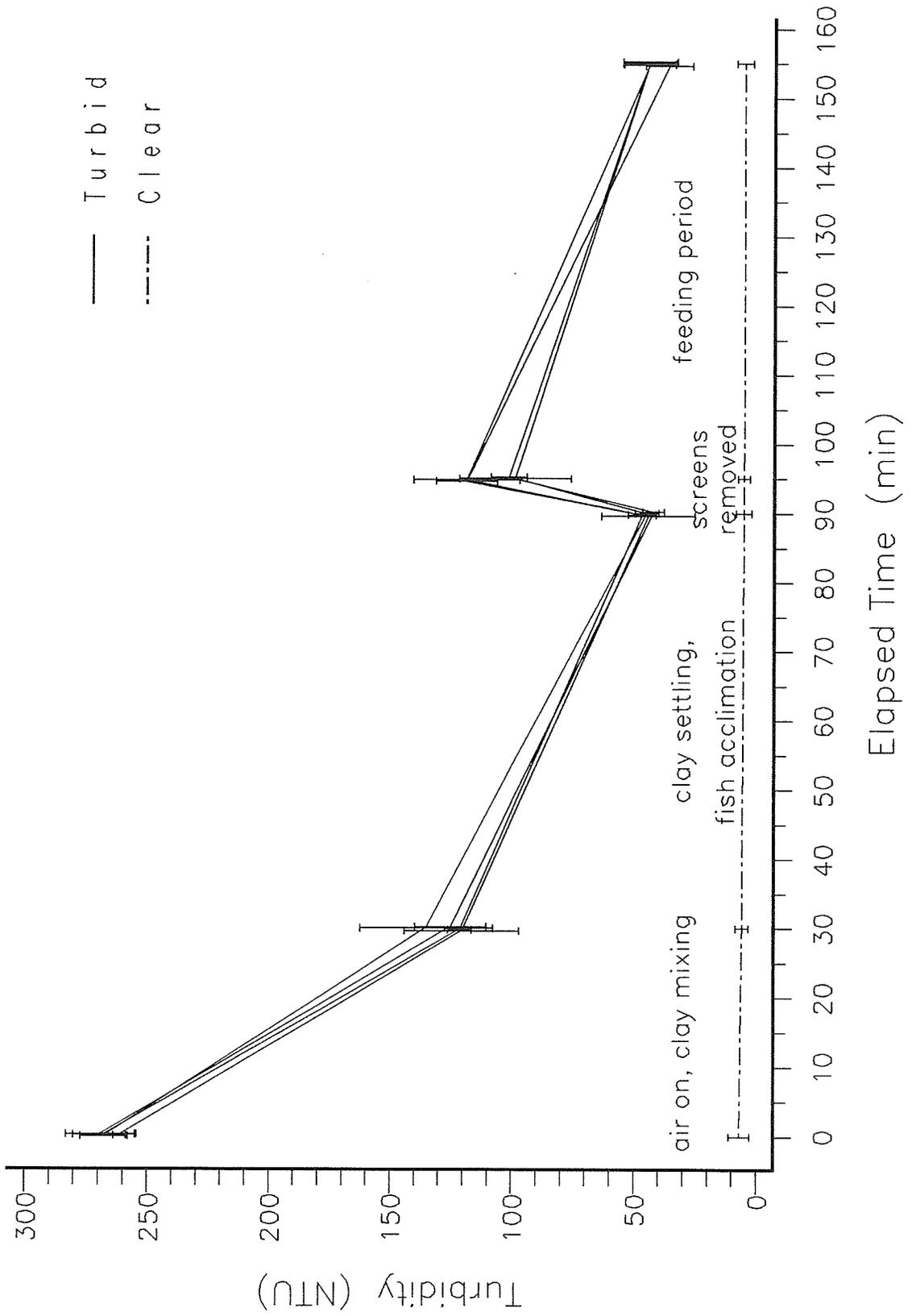
The experimental procedure was successful at producing consistent turbidity levels for each run within a trial. In all but one sample of the four turbid aquaria made during each run of the experiment, coefficients of variation were less than 30 % (Table 1), an acceptable level of within-sample variability (Elliott 1977). Turbidity estimates are given for samples from the third trial only; these values are representative of those obtained for all trials. At each time of estimation, mean turbidity was not significantly different among the four runs within a trial (ANOVA, $p \gg 0.05$; Table 1). Therefore within- and between-run variations in turbidity were low and about equal (F-values were close to unity). Figure 3 shows the change in turbidity over the duration of the experiment and the strong similarity of turbidity estimates from different runs. Non-turbid aquaria were also very consistent; mean turbidity throughout the experiment was 5.8 ± 1.5 (NTU ± 95 % CI).

Pike and walleye occur together in lakes in central Canada with water clarities ranging from 0.25 m to 3 m secchi depth (Craig and Babaluk 1989). Turbidity levels produced during the experiment (mean of 60 - 80 NTU during the feeding period) were very similar to those measured in Dauphin Lake (Table 2). Secchi depth in this lake is less than 0.5 m throughout the open water season, and averages 0.25 m

Ch. III, Table 1. Mean turbidity (NTU), coefficient of variation (%), and results of ANOVA testing for differences in mean turbidity between the four runs during the third trial (August 14-15, 1988). All means are based on estimates from four turbid aquaria unless otherwise indicated by the number in parentheses. The increased turbidity between 90 and 95 minutes resulted from a stir-up when the aquaria partitions were removed (see Methods section).

Elapsed Time (min)	Mean Turbidity (NTU)	Coeff. Var. (%)	F-value	prob. > F
0	267.5	3.6	0.40	0.76
	267.5	1.0		
	268.8	5.4		
	261.3	5.4		
30	135.0	20.2	0.46	0.72
	120.5	19.6		
	121.3	4.0		
	125.0	11.8		
90	45.0	10.6	0.11	0.95
	44.5	42.8		
	47.0	12.0		
	42.3 (3)	9.0		
95	98.8	23.2	1.39	0.30
	118.8	10.6		
	118.8	18.4		
	101.3 (3)	6.4		
155	44.3 (3)	21.0	0.58	0.64
	36.3	26.8		
	44.3	23.8		
	44.0	25.4		

Ch. III, Figure 3. Change in turbidity (NTU) over an experimental run. Solid lines connect means of point estimates of turbidity ($\text{NTU} \pm \text{s.e.}$) for four turbid aquaria from each of the four runs during the third trial (August 14-15, 1988). Estimates of NTU in non-turbid aquaria are means ($\pm \text{s.e.}$) of four estimates, one from each run within the trial. The steps of the experimental procedure taken between each sampling time are also shown.



Ch. III, Table 2. Turbidity (NTU) estimates for water samples collected at two locations, under varying wind conditions in 1988. Water samples from Dauphin Lake were collected inshore (depth < 1 m) about 10 cm below the surface. Pond samples were collected at the same 10 cm depth from one of four walleye rearing ponds at the Methley Beach Research Station.

Date and Time	Wind Speed (kph)	Turbidity (NTU)	
		Dauphin Lake	Rearing Pond
15 June 08:30	18	45	3.1
15 June 12:00	15	45	3.9
15 June 21:30	5	30	-
20 June 16:00	25	90	5.0
01 July 16:00	25	90	4.0
07 July 16:00	30	100	4.8
29 July 16:00	20	110	6.1
31 July	15	90	4.2

(Schaap 1987). Clear aquaria had low turbidity levels similar to those in the walleye rearing ponds at the Research Station (Table 2). These are clear ponds in which secchi readings often reach maximum depth (2.0 - 2.2 m; personal observation), and are therefore similar in clarity to mesotrophic lakes typically containing pike and walleye (Johnson et al. 1977). Therefore experimental water clarities were representative of those experienced in the natural environment by juvenile pike and walleye.

Forage Fish Size Estimates

Regressions calculated for each period of preservation for fathead minnows were not significantly different (ANCOVA; $p > 0.10$ for both slope and intercept differences), so the data were pooled. All spottail shiners were measured after equal periods of preservation. Relationships between fork length and pharyngeal GAP were linear and highly significant (Table 3; Appendix 2), and differed in slope between the two species (ANCOVA, $p < 0.001$). Wet weight was a power function of pharyngeal GAP for both species. Thus regressions were log-log linear, and also highly significant (Table 3; Appendix 2). Although the regression slopes were the same for the two species (ANCOVA, $p = 0.09$), intercepts were significantly different ($p < 0.001$). The good fit of the data resulted in narrow 95 % confidence belts (Appendix 2), which give the 95 % confidence interval for any future estimate of fresh fork length and weight using these regressions (Sokal and Rohlf 1981).

Ch. III, Table 3. Regression equations with associated R^2 and significance levels for relationships between fresh fork length (FL) and wet weight (WT) versus left pharyngeal total length (GAP).

Measure	Fathead minnows	Spottail shiners
Fork length	$FL = -2.098 + 16.585 (GAP)$ $R^2 = 0.96 \quad p < 0.001$	$FL = 0.942 + 15.185 (GAP)$ $R^2 = 0.93 \quad p < 0.001$
Wet weight	$WT = 0.0278 (GAP)^{3.249}$ $R^2 = 0.96 \quad p < 0.001$	$WT = 0.0357 (GAP)^{3.080}$ $R^2 = 0.93 \quad p < 0.001$

Even at the largest and smallest values of GAP, where confidence intervals for estimates are widest, the estimates for fresh fork length are ± 0.5 mm and ± 1 mm for fathead minnows and spottail shiners respectively. For weight estimates the widest confidence intervals are ± 0.010 g and ± 0.012 g for fathead minnows and spottail shiners, respectively. Thus these relationships have good predictive capability for estimating forage fish size from the pharyngeal GAP of forage fish consumed by pike and walleye during the experiment. The length frequency distributions of forage fish available in each trial, pooled across all aquaria, are illustrated in Appendix 3. The size of the forage fish, as a percent of mean pike and walleye fork lengths in each trial ranged from 19 to 31 % (Table 4).

Feeding Success

Pike were significantly larger in fork length and weight than walleye in each of the three trials (t-tests, $p < 0.001$). Fish of both species were significantly larger in length and weight with each successive trial (Table 4). These between-species and between-trial differences in fish size illustrate the necessity of standardizing measures of foraging success by predator size.

General Results

In the first two trials there were no differences in response to day and evening light levels for any species x water clarity combination

Ch. III, Table 4. Mean (\pm 95 % CI) fork length (mm) and wet weight (g) of pike and walleye in each trial of the feeding experiment. Mean sizes in each row are significantly different among trials at the p-levels shown. Prey size relative to pike and walleye fork length in each trial is given in parentheses as the mean forage fish fork length as a percent of mean predator fork length. N-values are given under mean weights and are the same for fork lengths.

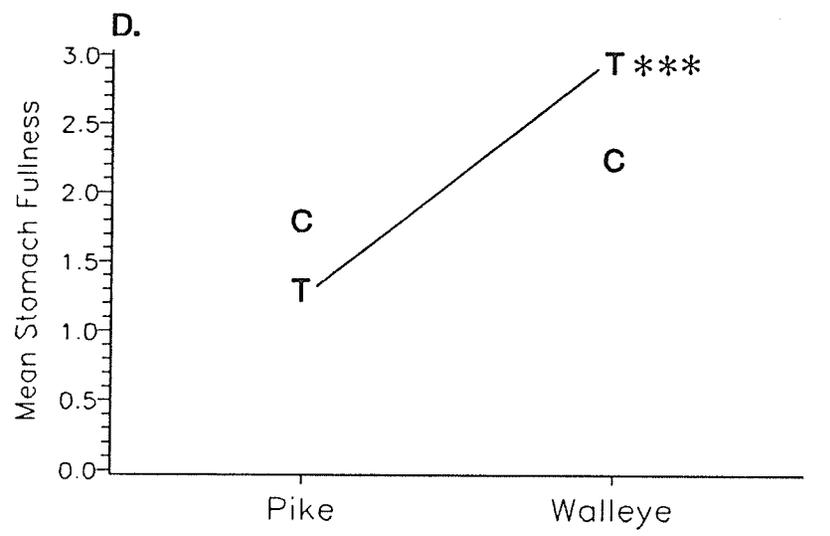
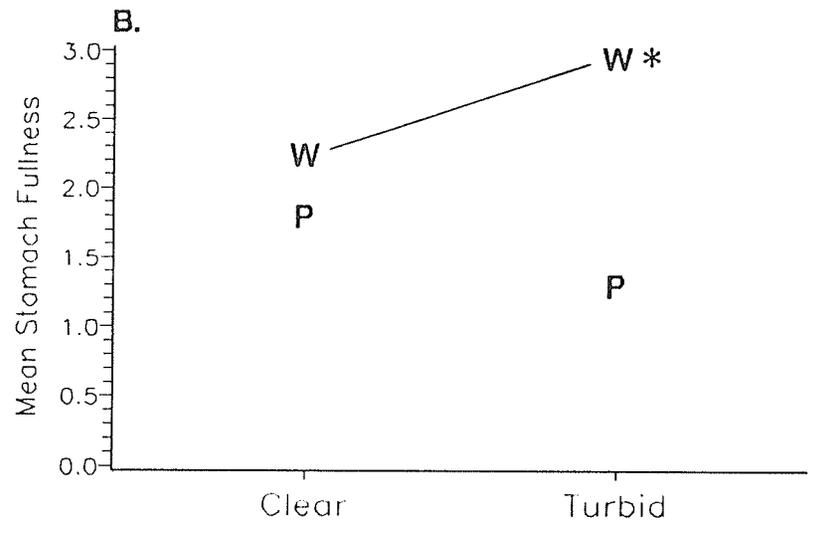
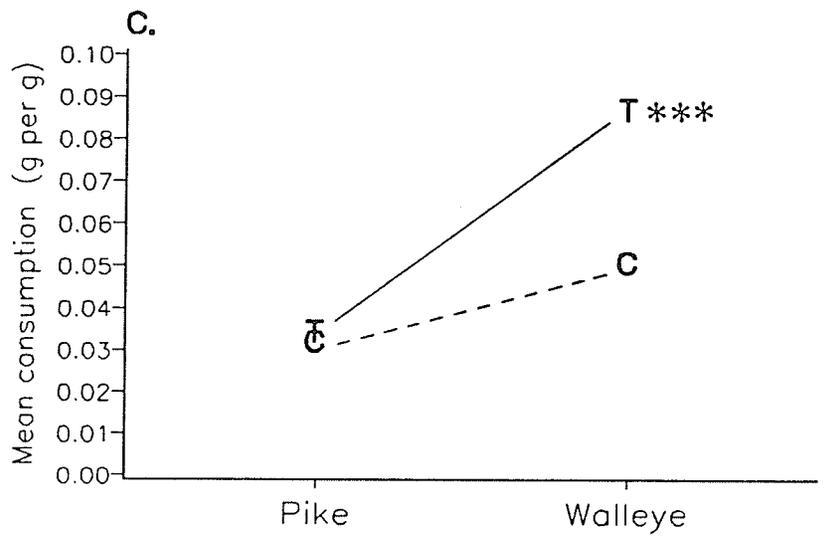
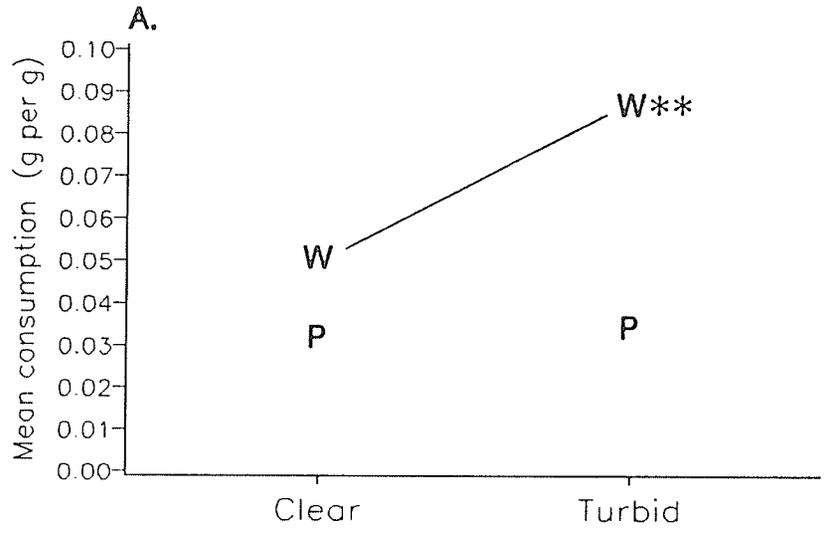
Measure	Trial			Difference Between Trials
	1	2	3	
<u>Fork length</u>				
Walleye	66.5 \pm 1.1 (26 %)	70.4 \pm 1.4 (31 %)	90.5 \pm 1.4 (30 %)	p < 0.01
Pike	91.5 \pm 3.0 (19 %)	117.8 \pm 5.3 (20 %)	129.1 \pm 4.1 (21 %)	p < 0.01
<u>Weight</u>				
Walleye	2.8 \pm 0.1 (48)	3.3 \pm 0.3 (56)	6.9 \pm 0.3 (48)	p < 0.05
Pike	5.1 \pm 0.6 (48)	11.1 \pm 1.2 (56)	14.0 \pm 1.1 (48)	p < 0.01

(split plot ANOVA, $p > 0.05$). Furthermore, there were no significant interactions between light level and other treatments, or between block and treatment effects. Therefore the first two trials were analyzed as a blocked 2 x 2 factorial design (Appendix 4). In the third trial there were significant interactions among light level, species and water clarity, but again no significant block x treatment interactions. Therefore split plot ANOVA was used for this trial (Appendix 4). The results from the first two trials were very similar and will be outlined together before a summary of those from the third trial.

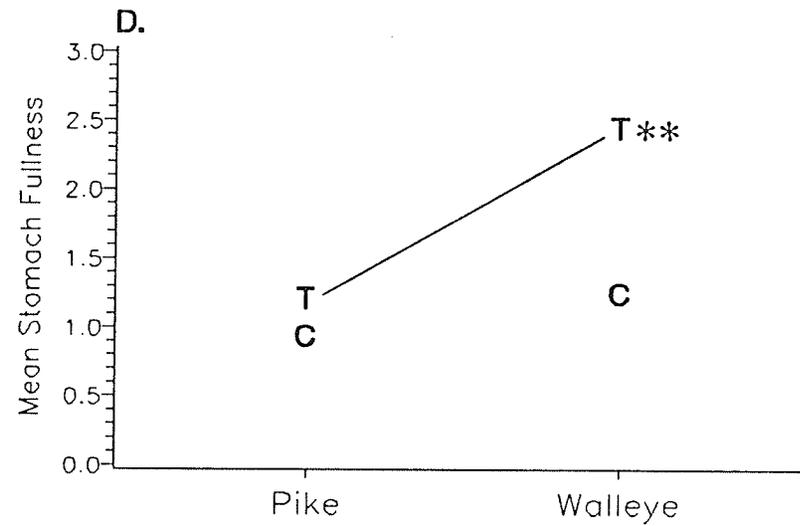
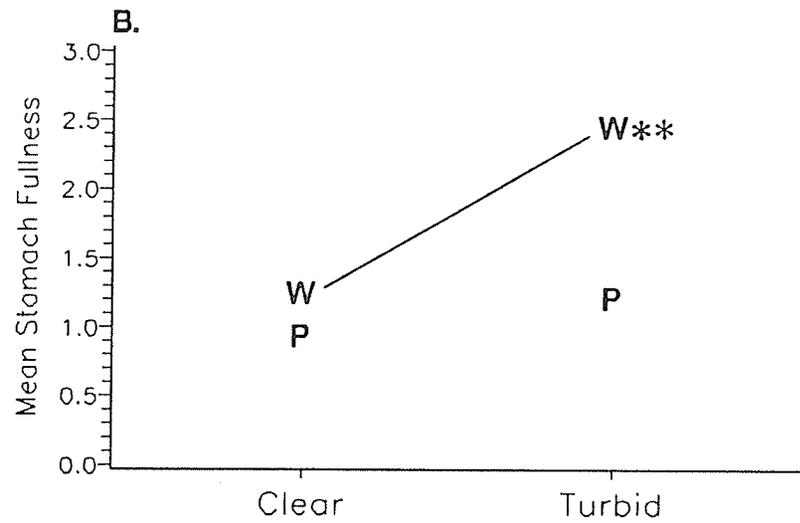
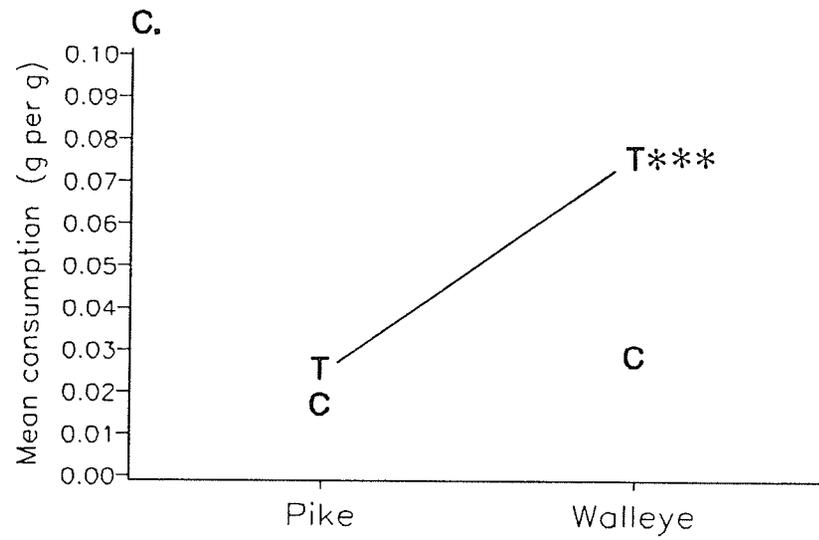
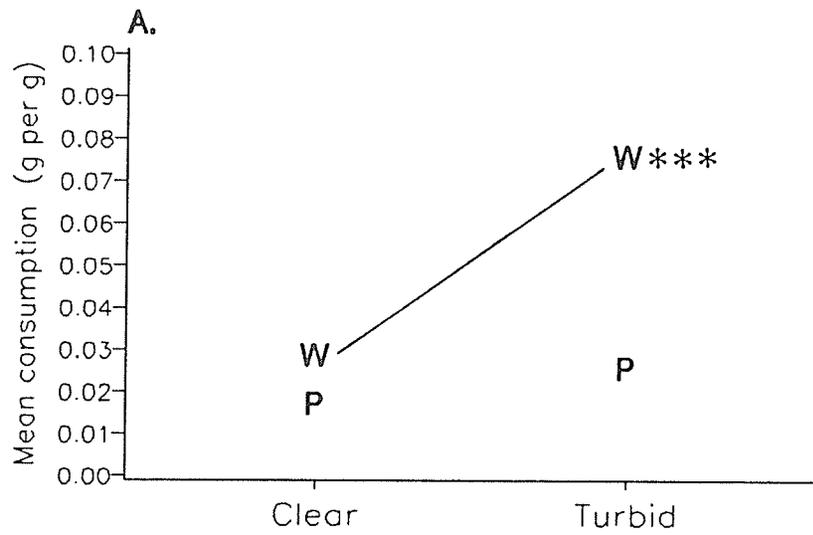
Trials 1 (July 3-4) and 2 (July 21-22)

Species and water clarity effects were both dependent on the level of the other factor in trials 1 and 2. Figures 4 and 5 present the results of the comparisons of simple effects for each treatment factor within the two levels of the other. Although the four treatment comparisons were not orthogonal, they were tested because significant species x water clarity interaction was evidence of real treatment differences among simple effects. Steel and Torrie (1980) state that non-orthogonal tests of simple effects are justified in this situation, and the probability of making a Type I error is protected by making only pre-planned comparisons. The direction of the differences was consistent for mean weight of consumed forage fish and mean stomach fullness, both within and between trials. Water clarity had no detectable effect on pike feeding in either trial (Figs. 4, 5). Walleye mean consumption and stomach fullness were higher in turbid compared to non-turbid waters,

Ch. III, Figure 4. Interaction plots showing least squares treatment means from the first trial of the feeding experiment, July 3-4, 1988. Mean consumption (g prey per g northern pike or walleye) and mean stomach fullness for each species are compared between clear versus turbid treatments in A and B, respectively. Mean consumption and mean stomach fullness are compared between pike and walleye within each water clarity in C and D, respectively. Solid lines join significantly different means at the p-levels indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$); broken lines indicate a marginally significant difference ($.10 > p > 0.05$).



Ch. III, Figure 5. Interaction plots showing least squares treatment means from the second trial of the feeding experiment, July 21-22, 1988. Mean consumption (g prey per g northern pike or walleye) and mean stomach fullness for each species are compared between clear versus turbid treatments in A and B, respectively. Mean consumption and mean stomach fullness are compared between pike and walleye within each water clarity in C and D, respectively. Solid lines join significantly different means at the p-levels indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

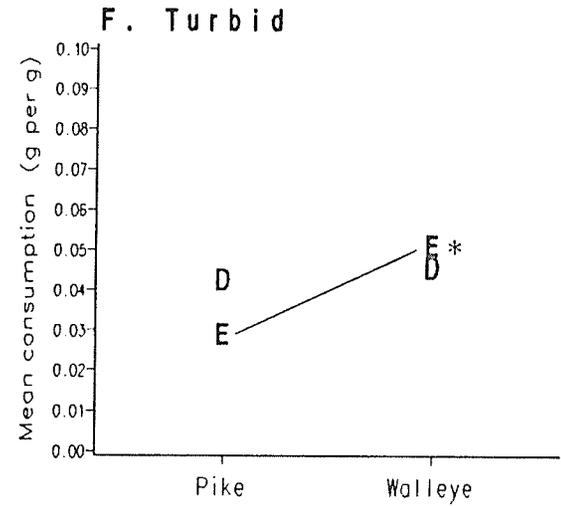
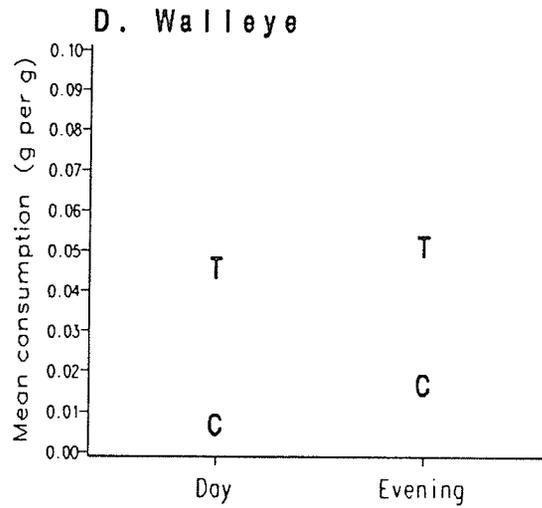
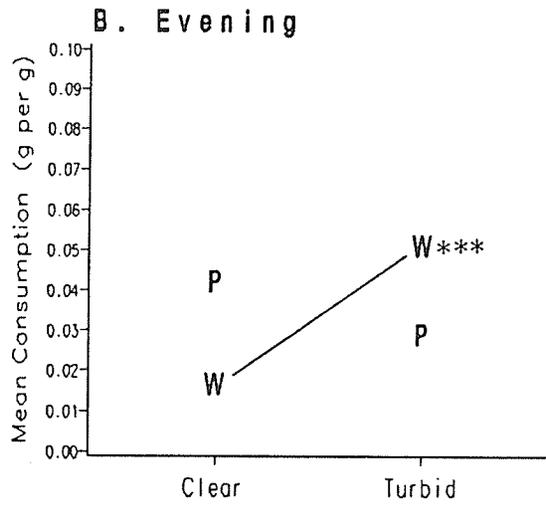
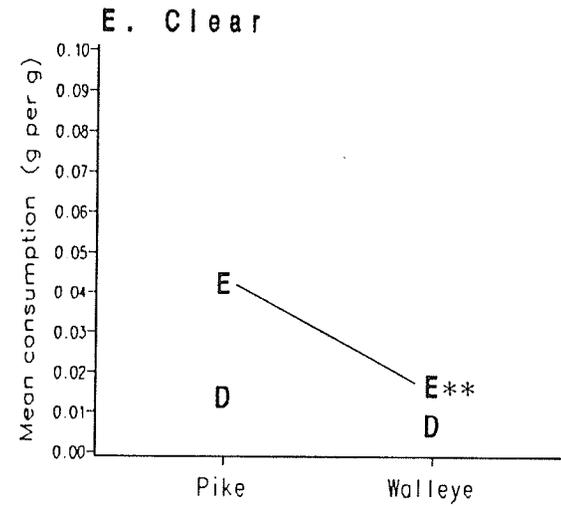
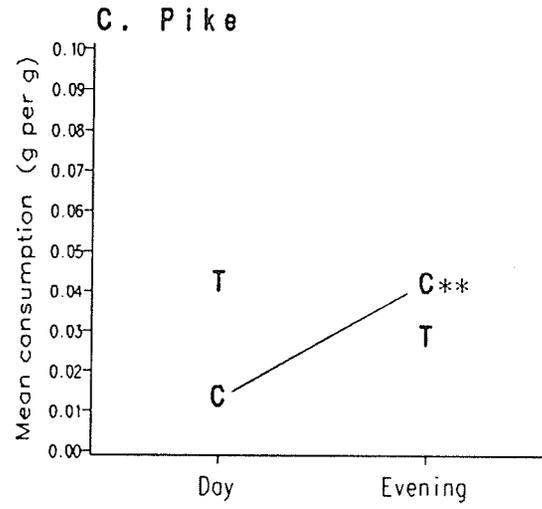
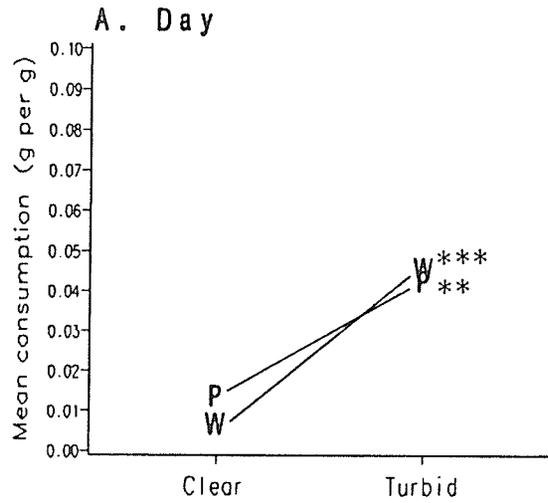


a difference that was highly significant in both trials (Figs. 4 and 5). For both measures, this difference between clear and turbid conditions was more pronounced with the larger, older walleye in the second trial (cf. Figs. 4 and 5). In non-turbid water, walleye mean consumption and stomach fullness were greater than that for pike, but the difference was not significant. Lastly, foraging success in turbid water was significantly higher for walleye than pike in both trials, and for both measures (Figs. 4 and 5).

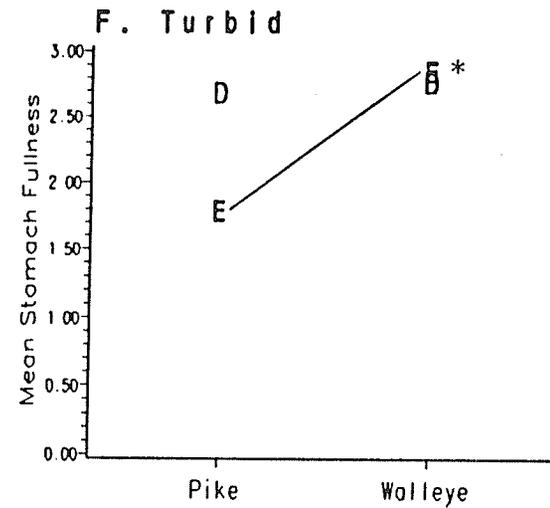
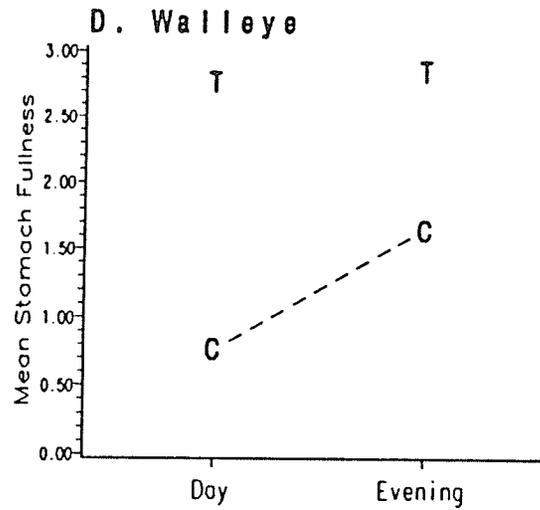
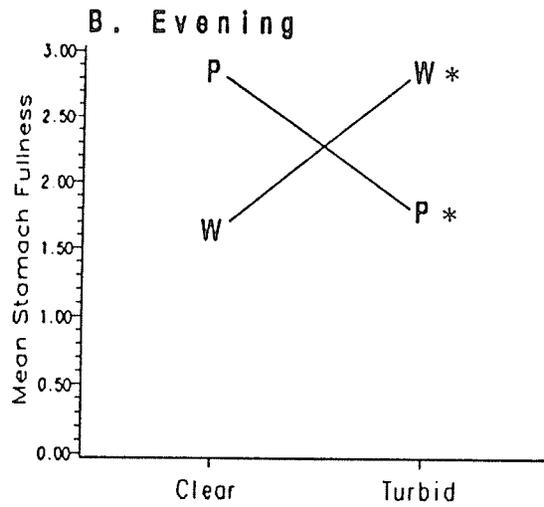
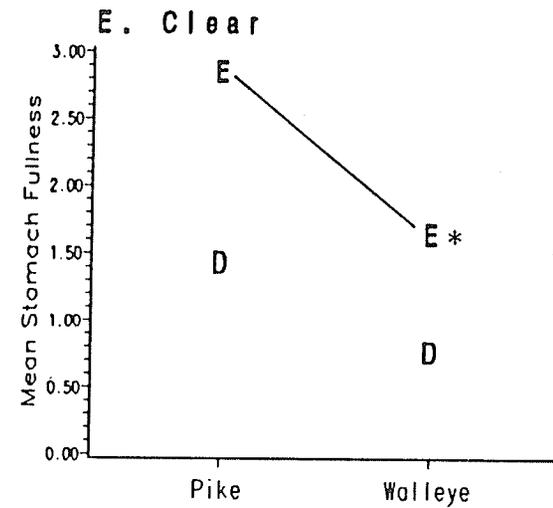
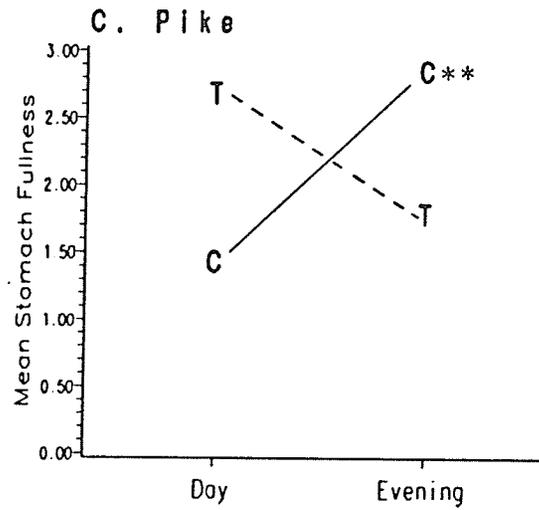
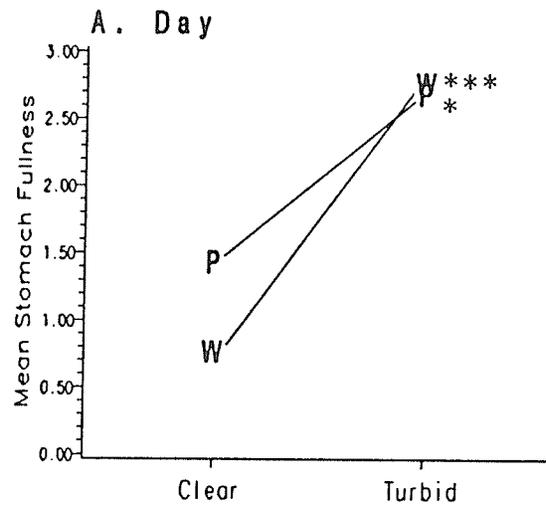
Trial 3 - August 14-15

Significant interaction amongst effects in the overall split plot ANOVA indicated that responses to each treatment were dependent on the levels of the other two. Thus simple effects of light level, water clarity and species were each contrasted within combinations of the other two factors (Figs. 6 and 7). This required 12 one degree of freedom (df) comparisons between subclass treatment means. These comparisons are again non-orthogonal, since their total df (12) exceeds the total for all effects in the model (9 df; Appendix 4). The same justification made earlier with regards to making non-orthogonal comparisons of simple effects as a consequence of significant interaction applies for this analysis as well. The results of these comparisons are presented in Figures 6 and 7. In non-turbid conditions, pike foraging success was significantly better under evening compared to daylight levels. In the turbid water, mean consumption and stomach fullness were slightly higher in the day versus evening runs for this

Ch. III, Figure 6. Interaction plots of least squares treatment means of mean weight of forage fish consumed per g predator in the third trial, August 14-15, 1988. Comparisons were made of simple effects within each level of the other factors. Clear versus turbid treatments were compared for each species in day (A) and evening (B) runs. Day versus evening treatments were contrasted for pike (C) and walleye (D) in each water clarity. Pike versus walleye foraging success was compared in clear (E) and turbid (F) water at each time of day. Solid lines join significantly different means at the p-levels indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).



Ch. III, Figure 7. Interaction plots of least squares treatment means of stomach fullness index in the third trial, August 14-15, 1988. Comparisons were made of simple effects within each level of the other factors. Clear versus turbid treatments were compared for each species in day (A) and evening (B) runs. Day versus evening treatments were contrasted for pike (C) and walleye (D) in each water clarity. Pike versus walleye foraging success was compared in clear (E) and turbid (F) water at each time of day. Solid lines join significantly different means at the p-levels indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$); broken lines indicate a marginally significant difference ($.10 > p > 0.05$).



species, although the differences were not significant ($p = 0.28$, $p = 0.085$, respectively). Water clarity had a significant effect on walleye feeding at both times of day. As in the first two trials, prey capture was significantly higher in turbid conditions. For pike, mean consumption and stomach fullness were highest in turbid water during the day. The opposite result occurred in the evening; pike mean stomach fullness was significantly higher in non-turbid conditions (Fig. 7). Time of day had no detectable effect on walleye feeding in clear or turbid conditions. Between-species differences were only significant during the evening portion of this trial. Pike had significantly higher mean consumption and stomach fullness than walleye in clear water; walleye were more successful than pike in turbid water.

Differences between trials

One problem with comparing foraging success between fish of different sizes is that their maximum rations differ. Furthermore, there is no way to measure requirements or 'need' by either of the measures that I used. Maximum ration declines with increasing size of fish (Elliott 1975), so consumption of forage fish per g predator weight was an inappropriate measure for between-trial comparisons. Stomach fullness may be a reasonable estimate however, if it can be assumed that the fish were attempting to feed to satiation. This assumption may be valid, given that they had been deprived of food prior to each trial.

There were no marked changes over the three trials in the direction or degree of any treatment differences for pike. Mean

consumption and stomach fullness were generally higher in turbid versus clear conditions. Although this difference was only significant in the third trial for feeding under daylight levels, the trend itself was unexpected, given the adaptations that pike have for feeding in a non-turbid environment. It was only during the evening feeding period in the last trial that pike feeding may have been more successful in clear compared to turbid water. The difference in mean stomach fullness was significant in this case, but not the difference in weight of consumed forage fish per g body weight.

Changes in walleye foraging success over the three trials were more apparent, and as predicted. Mean consumption and stomach fullness were consistently highest in turbid conditions, and the improvement relative to foraging success in non-turbid conditions increased with each trial (Figs. 4 - 7). This was mainly due to decreased foraging success in clear water with each successive trial, evidence that negative phototaxis increased with the increasing size and age of the walleye. Mean stomach fullness was the better measure for comparing foraging success among trials than mean consumption on a per g basis, as I noted above. Walleye consumption on a per g basis did decrease with each trial under all conditions, whereas mean stomach fullness values in turbid water were consistent across trials (ANOVA, $p > 0.05$, Figs. 4 - 7). In clear water however, mean stomach fullness was significantly lower in the second and third trials than in the first ($p < 0.04$); the second and third trials were not significantly different ($p = 0.78$). This indicates that foraging was increasingly limited by high light levels in clear conditions, whereas most walleye in turbid water had

full stomachs at the end of each trial. Despite this inhibition by the ambient light level in clear water, it was not until the third trial with the largest experimental fish that pike were more successful than walleye under these conditions. This result was presumably due in part to the unexpectedly low feeding rate for pike in clear water, and not only the increased negative phototaxis of the walleye.

DISCUSSION

The hypothesis that relative foraging success of YOY pike and walleye changes with different levels of light availability was supported. The results were not all in accordance with predictions however, and the effect of ambient light level was apparent only in the third trial. Walleye were able to forage most effectively in turbid conditions, an ability that improved most markedly between the first and second trial (see Figs. 4 - 7). Unexpectedly there was no detectable difference in pike foraging success between clear and turbid treatments. Only the pike under evening light levels in the third trial had more success in clear compared to turbid conditions; the difference was statistically significant for mean stomach fullness. I will first address a few points concerning the experimental conditions before discussing these findings and their implications.

An important criterion for this experiment's validity was that water clarity levels be similar to those encountered by both species in the natural environment. This was supported by the fact that experimental turbidity levels were in the same range as those recorded in Dauphin

Lake. Pike and walleye coexist in highly turbid environments such as Dauphin Lake, and both species inhabit clear lakes as well, where secchi depths are in the range of 2 - 3 m (Johnson et al. 1977; Craig and Babaluk 1989).

The turbidity level dropped by about 50 % during the feeding period (Fig. 3). To avoid disturbance, all water samples were collected near the water surface, where the decline in turbidity due to settling of suspended particles would have been most rapid. No samples were taken at lower depths in the aquaria, therefore the turbidity levels actually experienced by the fish may have been underestimated. Activity of the fish probably maintained more consistent mixing in the bottom portion of the tanks. The change in turbidity experienced by the experimental fish did not greatly exceed what might be encountered in a turbid natural environment. It is not unusual for turbidity levels to fluctuate markedly within a short timespan in Dauphin Lake, a shallow prairie lake which is almost constantly mixed by wave action (Table 2). It is important to note that the decline was consistent across all trials and therefore experienced by all fish, and equally importantly, that turbidity levels at each point of sampling were very consistent for the four runs within each trial (Table 1).

The assumption was made that neither pike nor walleye consumed enough forage fish to reduce their foraging success by decreasing prey availability. In the second and third trials, the number of forage fish was reduced by approximately 15 % on average, and never by more than 40 %. In the first trial the percent of available forage fish that were consumed in each aquarium averaged 34 %, a much higher rate. In four of

six turbid aquaria, walleye captured more than 50 % of the available prey during the one hour feeding period; this occurred in two aquaria with pike as well. However I feel that it is unlikely that this markedly affected the results. Even if walleye in turbid water were affected by reduced prey density towards the end of the feeding period, their success under these conditions was still well above that of all other treatment groups in this first and later trials. No other species x water clarity treatment group consistently reduced prey density to the point that prey availability should be suspected as a factor that influenced foraging success. Therefore the conclusion is that the differences in foraging success were a result of differential foraging ability under varying treatment conditions, and not a response to changes in prey availability.

It was assumed that neither predator species was given an advantage by being provided with a forage fish species that it could capture more efficiently than could the other predator. Juvenile pike and walleye both readily consume soft-rayed forage fish, including fathead minnows and spottail shiners (Colby et al. 1979; Robinson 1989). Mean fork length of forage fish in all trials was approximately 20 % of the average fork length of pike, and 25 - 30 % of mean walleye fork length (Table 4). Studies of juvenile pike and walleye prey selectivity have found that both species utilize prey of a wide size range but primarily consume fish that are 20 - 45 % of their body length (Beyerle and Williams 1968; Nursall 1973; Colby et al. 1979; Knight et al. 1984). Therefore, given this and the wide size range of forage fish available in each aquarium (see Appendix 3), it was assumed that an optimal prey

size was provided to both species, despite the size differences between pike and walleye in each trial.

Feeding Success

Estimates of individual forage fish weights were made using calculated regression equations relating fresh weight to pharyngeal GAP. The 95 % confidence intervals for an estimate, even at their widest point, was the estimated weight ± 0.012 g. As a percent of estimated weight, this could be an associated error of anywhere from approximately ± 2 to ± 40 %, since the range of estimated individual weights was 0.035 to 0.810 g. Weights estimated from GAP lengths closer to the mean would be narrower. There should not be a bias for any one treatment group however, since this applies to all forage fish size estimates.

Fish with an equal weight of prey fish consumed per g may not have been equally satiated, since this measure is insensitive to differences in relative stomach capacity for fish of approximately equal size. Another potential problem is that this measure may have been biased in favour of walleye because of their significantly smaller size in each trial. A pike that fed to satiation would probably have a lower weight of forage consumed per g body weight, compared to a satiated walleye in the same trial. For these reasons I assessed the degree of satiation as well, using an index of stomach fullness as a second measure of foraging success. It is more representative of foraging success if the above-mentioned biases exist, and hence is especially useful for comparisons between species. The main problems with this measure are that it may not

reflect food requirements (as already discussed), it is subjective, and it is a discrete rather than continuous variable. The full range of stomach fullness was represented by only four values (0 - 3), therefore a fish with a completely full and sometimes distended stomach was assigned the same value as those with stomachs only approaching fullness (> 75 % full). In contrast, mean consumption would not be subject to this discontinuity.

The strong similarity in patterns of mean consumption and mean stomach fullness for each treatment group in all trials indicated that the bias associated with size-specific maximum rations may not have been serious. If walleye had a higher prey consumption (g per g body weight) than pike solely because of their smaller size, and not better foraging success, then I would expect stomach fullness to be equal for the two species, ie. both achieved the same degree of satiation, assuming both were attempting to fill their stomachs following food deprivation. Therefore I believe that the similarities in stomach fullness and consumption reflect real differences in foraging success. This lends confidence to the conclusion that both variables adequately reflect differences due to real treatment effects rather than measurement biases. The nature of these treatment differences will now be discussed.

Pike

Pike foraging success did not depend on water clarity in the first or second trial. Mean consumption and stomach fullness were in fact slightly higher in turbid water, with one exception (Fig. 4b). Under

daylight levels in the third trial, both measures were significantly higher in turbid compared to clear conditions. These results were unexpected because pike are thought to be visually adapted to a clear environment (Ali and Klyne 1985). It was also predicted that higher light availability during daylight experiments should improve foraging success for pike in turbid conditions. But this effect was exhibited only in the third trial and only with marginal significance (Figs. 6 and 7). These results indicate that foraging was in some way more inhibited when light levels were highest. It is unlikely that visibility of prey was better in turbid water, since the contrast of objects viewed against background light is reduced as incoming natural light is rapidly attenuated by suspended particles in turbid water (Lythgoe 1978; Wetzel 1983). Mauck and Coble (1971) examined pike predation in turbid (secchi depth 13 - 20 cm) and clear ponds. As in this study, the number of prey consumed was higher in turbid ponds, but no explanation was given. A possible reason for the unexpectedly poor foraging success in clear conditions is pike territoriality. From the zooplanktivorous stage and onwards, juvenile and older fish are solitary and occupy individual home ranges (Frost and Kipling 1967). There were four pike in each aquarium in trials 1 and 2; perhaps space was limited such that agonistic interactions amongst individuals prevented normal independent foraging behaviour. Any strike manoeuvre towards prey fish could have resulted in the invasion of another pike's territory. Frost and Kipling (1967) observed that small (25 - 100 mm) pike in aquaria were aggressive when crowded, and tended to stay a discrete distance from others. Some pike attacked their own reflections seen in the mirrored side of an aquarium.

Their observations support the suggestion that pike require a minimum space that perhaps was not available in the aquaria used in this experiment. The potential for foraging inhibition by conspecifics was probably reduced in light-limited turbid water, since the ability to monitor each other's presence would have been reduced. Although the visibility of prey must also have been reduced, the evidence indicated that pike were able to capture forage fish in turbid waters. Information sensed by the lateral line probably aided prey detection under these conditions, since moving prey provide strong lateral line stimuli in the form of water displacements (Lythgoe 1978). Robinson (1989) suggested that the fathead minnow's habit of continuously changing direction was a primary cause of their high vulnerability to pike predation. Shoals of forage fish were on occasion observed circling the tanks continuously during the experiments. Fathead minnows and spottail shiners do not possess tapeta or other visual adaptations to low light availability. Therefore the pike's success in turbid water could also in part have been due to a reduced ability of the prey fish to detect their predators.

Pike foraging success was higher in clear compared to turbid conditions only in the third trial under evening light levels. There may have been less intraspecific interference in this case because there were only three pike in each aquarium, and ambient light levels were at the lower setting. During the day, foraging success was still highest in turbid water, presumably for the same reasons as those given above.

Only in the third trial did ambient light level have a significant effect on pike or walleye foraging success. I think that this effect was

obscured by unequal replication in the first two trials. Missing observations decreased the power of the statistical tests relative to that in the fully and equally replicated third trial. Another factor was the relatively small difference between the two light settings used for day and evening runs. As mentioned previously, outdoor light levels on bright midsummer days are much higher than those produced for this experiment. I think that the effect of ambient light would have proved more important for both species had higher intensity natural daylight levels been simulated.

Walleye

Foraging success in non-turbid conditions was the same for walleye and pike in trials 1 and 2; only in the evening period of the last trial were pike more successful than walleye under these conditions (Tables 5 and 6). This result was due in part to the low prey consumption by pike in clear water, but also a consequence of changes in walleye visual capabilities. The latter was evidenced by the significant decline in mean stomach fullness and the increased difference for both measures between clear and turbid conditions with successive trials. Walleye are a shoaling species, especially during the juvenile and subadult stages (Johnson 1969; Ryder 1977). Shoaling behaviour is thought to aid foraging success (Pitcher et al. 1982; Pitcher 1986). Lower prey consumption by walleye in clear conditions can thus not be attributed to territorial aggression, as it was for pike. The changes seen with increasing size of walleye in each trial support the conclusion that

increased negative phototaxis was the mechanism for poorer foraging success in clear water. The tapetum lucidum must have been at least partially developed in walleye in the first trial (mean fork length was 66.5 mm), because mean stomach fullness in turbid water was close to the maximum. Despite the presence of the tapetum however, walleye in the first trial fed to almost the same degree of satiation in clear as in turbid water (Fig. 4b). This indicates that higher light levels under these conditions did not yet adversely affect these smaller walleye to a great degree. By the next trial however, mean stomach fullness was significantly lower than in the first, and more reduced relative to that of walleye in turbid conditions. The change in mean size of walleye from these two trials was small but significant, (66.5 to 70.4 mm fork length), and corresponds well with the size at which an important change occurs in the developing walleye retina. The rod photoreceptors coalesce into bundles of 25 - 30 to form "macroreceptors", when walleye are about 60 - 70 mm long (Braekevelt et al. 1989). This occurs concomitant with tapetum development and functions to more efficiently direct light towards the sensory cells. The enhanced light transmission to the rods markedly increases sensitivity to high light levels. In the first trial, it is probable that some walleye had not yet developed macroreceptors. In the second trial when walleye averaged 70 mm, the presence of bundled rod cells in the retinae of most of the walleye would explain the decreased feeding in clear water, relative to the first trial. This would also explain why mean stomach fullness in clear water was depressed only slightly further in the third relative to the second trial, when walleye mean fork length was 90.5 mm. Although the tapetum

continues to develop until fish are 125 - 140 mm, the development of the macroreceptors marks the point at which the tapetum shows the greatest increase in visual sensitivity (Braekevelt et al. 1989; L. Vandenbyllaart, U. Manitoba, pers. commun.).

Given these changes with development exhibited by walleye in non-turbid water, the expectation was that foraging success in turbid conditions would show an accompanying improvement with each trial. This was not demonstrated; mean stomach fullness was always high in turbid water, evidence that in all trials some walleye fed to satiation. Improved vision in turbid conditions in later trials should have increased prey encounter rates and therefore capture rates, but whether the larger, older walleye become satiated earlier in the one hour feeding period than the smaller fish in the first trial could not be assessed in this experiment. Shortening the duration of experimental feeding would have enabled among-trial differences in the rate of prey capture to be more closely examined.

Implications for natural populations

This experiment yielded results that have implications for understanding the nature of potential interactions among YOY pike and walleye in the natural environment. The main inference to be made from this study is that YOY walleye should have better foraging success and therefore better growth than YOY pike in turbid, light-limited conditions. This advantage could lead to competitive dominance if walleye effectively exploited the food resource to an extent that limited its

availability to pike. Furthermore, better growth should result in a superior ability to escape size dependent predation and juvenile overwinter mortality, thus leading to stronger year classes (Werner 1986; Post and Evans 1989a; 1989b).

It is important to note that pike and walleye foraging success was equal in turbid conditions under daylight levels in the third trial. Furthermore, pike did capture prey under turbid experimental conditions in all trials, so the potential for competition in the natural environment would depend on the degree of turbidity, and whether the food resource is in limited supply. Pike in shallow, highly turbid prairie lakes appear to be limited by their visual capabilities, whereas walleye are not (Craig and Babaluk 1989). In somewhat less turbid or light limited environments, walleye may not have an advantage.

Although pike generally did not feed to satiation in turbid water, probably more would have been able to had the feeding period been longer. This would however require an increase in the energetic costs of foraging, and their growth efficiency would therefore probably be reduced in comparison to those living in a clear environment. A model of piscivore growth efficiency developed by Kerr (1971) provides theoretical support for this suggestion. He showed that decreased visibility can strongly reduce growth efficiency when prey are relatively large and rare. The natural prey of pike and walleye fall into this category, because of the shoaling tendency and patchy distribution of many cyprinid and other prey species (Nursall 1973; Ryder 1977). Under conditions of limited prey visibility and reduced prey encounter, pike may become more active to find food. Pike are recognized as being

sedentary "sit-and-wait" predators, normally inactive for the majority of the time (Frost and Kipling 1967; Diana 1980; pers. observ.). They are completely inactive at night, and adults can survive long periods without feeding (Diana 1980). Chapman and Mackay (1984) found however, that radio-tagged adult pike were more active on windy days and moved offshore. They suggested that the fish were avoiding areas of reduced visibility in the more turbid shallow littoral zone. I expect that YOY pike would be especially likely to become more active predators in light-limited conditions because they must feed more frequently than adults to satisfy higher energetic requirements due to their smaller size (Bevelheimer et al. 1983). This increased activity would increase search costs and reduce growth efficiency, ie. increased energy would be expended for activity, at the expense of energy available for growth. Walleye, in contrast, are active shoaling predators, so their superior visual capabilities in turbid conditions should reduce their search costs and hence improve growth. In this experiment, even the smallest walleye of the first trial had better foraging success than pike in the turbid aquaria. The implication is that any competitive advantage held by walleye in a turbid environment may commence early in their first summer, after the onset of walleye negative phototaxis. Unfortunately, I was unable to conduct experiments with smaller walleye that were just beginning to become negatively phototactic.

Lateral line sensory information may have been a means by which pike could detect their prey in the turbid water. This would partly explain why their foraging success was no different from that of pike in clear conditions. I think this similarity was more a result of poor

success in clear water however, a consequence of unnatural experimental conditions in terms of pike density. Furthermore, although the lateral line is the means by which pike orient towards their prey, they require visual contact to make a strike (Nikolsky 1963). Therefore the importance of vision and the evidence from other studies (eg. Vollestad et al. 1986; Craig and Babaluk 1989), lead me to conclude that pike should have reduced foraging success in turbid environments, although this was experimentally demonstrated in just one of the trials. More important than this comparison between pike in clear and turbid conditions is the finding that walleye had higher prey consumption (g per g body weight and stomach fullness) than pike in turbid water at all sizes, as already discussed.

The inferences that can be made from this experiment about competitive interactions in a non-turbid environment are less apparent. I predict however that pike would have better foraging ability in a clear natural environment than they did in this experiment. Neither species may have an advantage in clear water when both are positively phototactic. Walleye should be at a disadvantage with increasing negative phototaxis, and there was evidence of this in the last trial. However, this potential disadvantage should be reduced in the natural environment by interspecific differences in diel activity patterns. In clear lakes, negatively phototactic walleye are inactive during the day and often rest on the bottom; they forage crepuscularly or nocturnally when light levels are most favourable (Ryder 1977). This mechanism should allow walleye to be as equally effective predators as pike in a clear environment. Despite temporal separation in feeding activity, the

two species could still utilize the same food resource, so one species may still outcompete the other for a limited food supply (Holt 1987). Habitat separation can also help reduce or eliminate competition, but although walleye move offshore from the littoral zone once fully negatively phototactic, they still forage crepuscularly in the shallow littoral zone of clear lakes (Ryder 1977; Serns 1982b; this study). They may therefore still exploit the same prey resource as pike. Temporal and habitat segregation will reduce contact between competitors however, which is important if interference plays a role in determining competitive superiority. In the previous chapter, this was suggested to be the case for small pike and walleye. In clear conditions therefore, the greatest potential for interspecific competition perhaps exists when walleye are not yet fully negatively phototactic and there is the greatest overlap with pike in habitat and activity patterns, and thus the greatest potential for both exploitative and interference competition. Competitive dominance would then depend on factors other than light availability that affect relative foraging success. These include the relative size of the pike and walleye, the degree of resource limitation, and other elements of the environment that can affect interspecific interactions.

In conclusion, the experiment demonstrated that the relative foraging success of YOY pike and walleye depends on conditions of light availability and the stage of development of the walleye tapetum. A number of improvements to the experiment would enhance the degree to which these results can be extrapolated to natural populations. A better measure of foraging success would be obtained if size-specific maximum

rations could be determined for each species and actual consumption rates over a longer period were compared to their theoretical maxima. Increasing the number of turbidity levels would increase the scope of this experiment. Using larger aquaria or placing only one pike in each tank might reduce the effect that territoriality perhaps had on their foraging success. Lastly, it would be profitable to conduct trials with younger fish, since the smallest walleye in this trial were already past the size at which they had started to become negatively phototactic.

GENERAL DISCUSSION

GENERAL DISCUSSION

In this thesis I used three types of investigation to examine competitive interactions among young-of-the-year northern pike and walleye. By considering the results from each, a more complete analysis has been made because each yielded information not available from the others. The study of Whitefish Lake YOY pike and walleye demonstrated a potential for competition, the enclosure experiment detected the effects of competition on growth and survival and the feeding experiment examined one mechanism by which competitive dominance may be determined. I think that a number of valuable insights into the nature and importance of intraspecific and interspecific competition for these species can be derived from these results. Their applicability to natural populations is of course dependent on whether the experimental conditions under which the effects were demonstrated ever exist in natural systems. I have suggested in all three chapters that interactions between YOY pike and walleye may change in potential importance, direction, and intensity over the course of their first summer. Thus I will synthesize my results by discussing the likelihood and potential outcome of competition between YOY pike and walleye, as it may change at different stages and under different environmental conditions.

The results of the enclosure experiment indicated that interspecific competition was most pronounced during the early juvenile period. The size advantage of pike in agonistic interactions and prey consumption was inferred as an important means by which they outcompeted walleye for the available forage fish. In Whitefish Lake, pike were

larger than the walleye throughout the summer and presumably would be in many years, since pike usually spawn before walleye in the spring (Scott and Crossman 1973). Pike may also have had a visual advantage since the walleye in the enclosures (a clear environment) were large enough to have been undergoing the transition to negative phototaxis. The laboratory feeding experiment did not yield conclusive results with respect to relative foraging success of YOY pike and walleye in a clear environment, but I think that this was a consequence of the pike being negatively affected by the presence of other pike in the tanks. If it can be assumed that pike do have better foraging success in clear compared to turbid waters under more natural conditions, then pike may have had an advantage over walleye in prey capture. I would also expect pike to be the dominant species when walleye are still positively phototactic. This is again because of pike's size advantage and because there is the greatest overlap in habitat and temporal activity patterns of YOY pike and walleye during the early juvenile period. In Whitefish Lake, both species were caught inshore at all times of day only during the early summer.

Later in the summer however, temporal and habitat segregation may reduce interspecific interactions. Of the three trials of the enclosure experiment for which competition was demonstrated, the one with the largest, oldest fish ended with equal effects of intraspecific and interspecific competition for both species. I suggest that temporal differences in activity prevented agonistic interactions, and the same may be true in the natural environment. Once they became negatively phototactic, walleye that are offshore during the day move inshore to

feed after dusk (Ryder 1977; Serns 1982b). By foraging in clear, shallow water when light levels are most suitable, walleye can reduce contact with diurnal competitors and predators, and avoid the high daytime light intensities to which they are sensitive. The prey resource may still be shared despite temporal separation however, so it is difficult to predict which species may be the better competitor under these conditions. It would depend on other factors such as the nature and availability of the prey resource, and the relative density and body sizes of pike and walleye.

In a turbid lake, interference may be reduced if pike can not effectively defend territories because of visual limitations. Walleye could be the dominant species under these conditions by merit of their smaller food requirements (Persson 1985), and especially once the tapetum begins to aid their prey capture success. Competition for prey may be prolonged in shallow, well-mixed, turbid lakes that lack the deeper offshore zone that larger, negatively phototactic walleye move to by mid to late summer in clearer lakes. Low light penetration and wave action limit aquatic vegetation abundance and there is little difference between the shallow littoral zone and the more offshore 'pelagic' habitat, even in large lakes. Turbidity may also reduce temporal separation in foraging activity, since both species would probably be most active during the day. Stang and Hubert (1984) found that walleye in a turbid prairie lake were evenly distributed both temporally and spatially. Pike stomachs were fullest at early morning and late afternoon in turbid Dauphin Lake (Craig and Babaluk 1989). Ryder (1977) suggested that adult and juvenile walleye become more diurnal in turbid

waters and Chapman and Mackay (1984) observed that pike in a shallow lake moved offshore on windy days to avoid the more turbid conditions of the littoral zone. These findings all indicate that both species are diurnal in light limited conditions. The results from my feeding experiment and those from other studies examining pike growth or body condition in turbid waters (eg. Vollestad et al. 1986; Craig and Babaluk 1989) support my suggestion that in turbid conditions, walleye should have better prey capture success and hence potentially be the superior species in competition for prey.

The apparent differences in importance of intraspecific and interspecific competition to each species outlined in Chapter II provides some insight into how the relative population densities of pike and walleye may influence competition. An important result in the enclosure experiment was that intraspecific effects on pike were always at least equal to and usually greater than interspecific effects from walleye. This leads to the prediction that walleye may not affect pike unless walleye is the more abundant species, because walleye have a smaller per-capita effect than pike on food resources. In contrast, fewer numbers of pike are required in order for them to have an effect on walleye, because of the advantages associated with their larger size. Thus the effects of pike on walleye demonstrated in the first two enclosure experiments may have been substantial even if pike density had been less than walleye density. This may explain why some introductions of pike fingerlings into walleye lakes have had a negative effect on the walleye while attempted introductions of walleye fingerlings into a pike dominated lake were unsuccessful until after the pike were removed

(Colby et al. 1987). In both situations, walleye did not seem to affect pike, whereas pike clearly had a negative impact on walleye. The mechanism could have been predation by adults rather than competition, but it is important to note that YOY competition, through its effect on growth and hence body size and condition, could predispose inferior competitors to predation by adult piscivores (Larkin 1956; Werner and Gilliam 1984; Werner 1986; Post and Evans 1989a). In food limited turbid environments, interspecific competition with walleye may be more important for pike than intraspecific competition, because the walleye could have a more severe impact on the prey resource. This would be due to their superior foraging success and presumably their higher growth rates, which would lessen the differences in body size and hence in per capita prey removal.

The foregoing predictions concerning competitive interactions between YOY pike and walleye will only be tenable if there is a real potential for competition to occur. I have pointed out throughout this thesis that competition will not be important unless a shared resource is in limited supply, regardless of how great the degree of niche overlap may be. This was clearly demonstrated in the last trial of the enclosure experiment. YOY pike and walleye overlapped completely in diet and habitat, but prey were in adequate supply and no competition was detected. Thus it is important to question whether YOY pike and walleye ever experience food limitation in the natural environment. This is difficult to assess. Temperature and other abiotic variables, and fish community structure and population density are just some of the factors that interact in their influences on food consumption. Despite

this complexity, the literature indicates that growth rates of fish in the natural environment are often less than experimentally determined maxima and are frequently related to prey availability (eg. review by Werner 1986).

Forney (1966) found that between year differences in YOY walleye growth after July 1 in Oneida Lake, New York, were more related to forage fish availability than temperature. There are few other examples of food limitation in YOY pike and walleye populations, but the evidence from other studies is pertinent. Individuals from stunted populations of perch (Alm 1946) and pike (Carbine 1944) showed an increase in growth rate when reared under laboratory conditions of food abundance. In freshwater lakes and streams, considerable evidence exists for a relationship between individual growth rates and prey availability, and studies of fish populations that have been 'thinned out' have often shown intra- and interspecific density dependence of growth (Alm 1946; Swenson and Smith 1976; Forney 1977; Johnson 1977; Persson 1985; LeCren 1987; Colby et al. 1987; Persson 1987a). Hanson and Leggett (1982; 1985) suggested that fish populations in the littoral zone of temperate lakes are often food limited. Boisclair and Leggett (1989) and Persson (1987a) have demonstrated a several fold variation in perch growth among lakes and among age-classes within lakes that can not be explained by temperature differences or other abiotic factors. In both studies, prey availability and prey type were the important influences on growth. Patches of zooplankton, emergence of aquatic insects, and hatches of larval prey fish can be discontinuous in time and space and therefore cause periods of food limitation for YOY fish. I suggested in Chapter I

that growth of YOY pike in Whitefish Lake may have been limited by diet quality, as shown by their utilization of invertebrate prey. YOY pike and walleye require prey of increasing size as they grow and are also more sensitive to discontinuities in prey size distribution because they can not utilize as broad a size range of prey as adults (MacLean and Magnuson 1977). The frequent observation that YOY pike and walleye continue to utilize invertebrates after becoming piscivorous also illustrates that preferred prey are not always available in sufficient quantity (Hunt and Carbine 1951; MacLean and Magnuson 1977; Knight et al. 1984; Hurley 1986; Chapman et al. 1989).

I conclude by suggesting that YOY pike and walleye probably do occasionally experience reduced prey abundance and quality in the natural environment and that they may in fact be more sensitive to this limitation than adult fish. Given this, it remains to be discussed how the results of my research can be used to explain some of the observed patterns of pike and walleye distribution in freshwater lakes.

The competition experiment demonstrated that strong negative effects can result when YOY pike and walleye share the same habitat and diet. There was limited opportunity for a change in diet in response to competition and no opportunity for a habitat switch. I realize that in this regard, the enclosures were an artificial representation of the natural environment, but I also think that there is an important conclusion to be drawn. The results suggest that YOY pike and walleye will probably not coexist, or will experience strong competition, in lakes where there is insufficient opportunity for segregation along some niche axis (eg. habitat, food, or temporal activity). Tonn and

Paszkowski (1987) related the simple habitat structure found in small lakes both to the habitat overlap and strong competitive interactions demonstrated between yellow perch and central mudminnows in two small northern Wisconsin lakes. Persson (1983; 1987b) showed that perch suffer increased competition with roach when perch are forced into the roach dominated pelagic zone by resource depletion in the preferred shallow littoral zone. With specific reference to pike and walleye, Johnson et al. (1977) found that Ontario lakes supporting pike and walleye are much larger on average (244 ha) than pike-only lakes (37 ha) and walleye-only lakes (66 ha). The authors suggested that the smaller lakes contained only one of the two species because these lakes did not allow for niche separation between pike and walleye. The great abundance of pike and pike-walleye lakes and the pike's wider geographical range (Scott and Crossman 1973), indicate that it is a more 'generalist' species than walleye, able to be successful in a wider variety of habitats and environmental conditions. Ryder and Kerr (1978) also noted that lakes containing walleye and not pike are far less common than the converse. This was attributed to the walleye's more 'rigorous requirements' (Ryder and Kerr 1978), which may be because walleye is the more recently evolved species and has a number of specializations not exhibited by pike (Collette et al. 1977). These include a physoclistous swim bladder, (an adaptation for a demersal existence in relatively deep waters), and the light sensitive tapetum which prevents them from being able to inhabit clear, shallow water bodies that offer no refuge from high light intensities (Collette et al. 1977). Walleye lakes in Ontario are fairly clear and on average are slightly deeper and have a smaller

littoral zone than pike lakes (Johnson et al. 1977). Presumably the availability of offshore deeper waters is reduced in small lakes, so the potential for coexistence is low and the majority of small lakes favour pike. Lake size and its associated habitat heterogeneity may therefore be an important indicator of the probability for pike and walleye to coexist (Colby et al. 1987). Another factor influencing habitat diversity is turbidity, as already discussed. In very shallow turbid lakes, competition may be more important because there is little opportunity for species segregation and walleye could be the dominant species because of their superior visual capabilities.

Predation and adverse abiotic factors reduce population density and can thus reduce food limitation, and therefore have often been cited as more important influences than competition (Connell 1975; Wiens 1977). It is an oversimplification to consider one factor as the only influence on a natural system however, especially in size structured fish populations, because different size classes of individuals influence others in varied and sometimes opposite ways (Roughgarden and Diamond 1986; Werner 1986). Predation can reduce competition through its direct effect on population density, but also can indirectly intensify competition by restricting competing species to habitats that provide cover from predators. Competition can reduce growth and condition and thereby increase vulnerability to adverse environmental conditions, or increase the length of time spent in a size range most susceptible to predation (Larkin 1956; Werner 1986; Post and Evans 1989a; 1989b). These interactions may be important consequences of competition among YOY pike and walleye in the early summer. Furthermore, competition may still be

important even when only intermittent in effect, because competition of even short duration could have a long term impact on population density, through the mechanisms just described. Therefore I think that competition may be more important among YOY than adult pike and walleye, whose greater flexibility of feeding habits and habitat use allow them to reduce the potential for food limitation (Colby et al. 1987). Moreover, flexible growth rates and high reproductive potential enable adult fish to withstand periods of competition, making competition less important than other population controls (Larkin 1956).

In this thesis I examined competition in isolation from other potentially important regulators of YOY pike and walleye growth and survival. My results are therefore not directly applicable to natural populations, because predation and environmental factors interact with competition and make its effects less pronounced. I also have not considered the importance of interactions among YOY pike and walleye and other potential competitors. Given the difficulty of detecting competition however, I feel that little would be gained by attempting to experimentally examine its importance relative to all other interactions that may influence YOY pike and walleye. I think that my experiments are useful because they provide some insight into the conditions for and outcome of competition between these species, which would not have been possible in the analysis of a more complex system. Understanding the nature and mechanisms of competition at a simpler level is an important first step for being able to make reliable predictions concerning its outcome in the natural environment, where other factors must be taken into account.

In conclusion, the work presented in this thesis provides a preliminary but nonetheless important investigation of the nature and direction of competitive interactions between YOY pike and walleye. The evidence that I have presented indicates that there is a potential for intraspecific and interspecific competition to have important effects on the growth and survival of both these species. Environmental conditions that influence such factors as the nature and availability of the prey resource and the relative body size, density, and foraging success of YOY pike and walleye, will determine competitive superiority as well as the intensity and long term impact of interactions.

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APPENDIX I

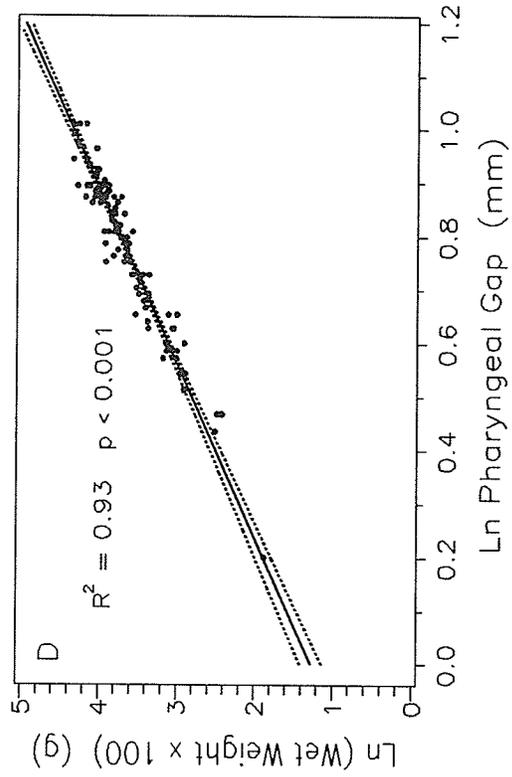
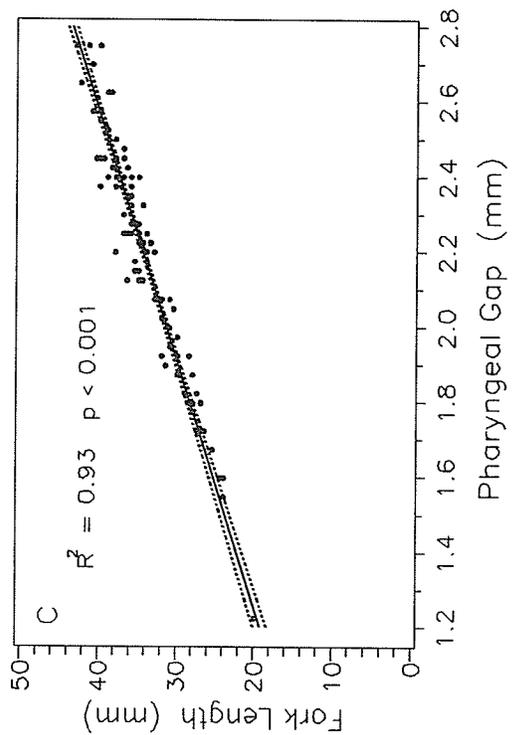
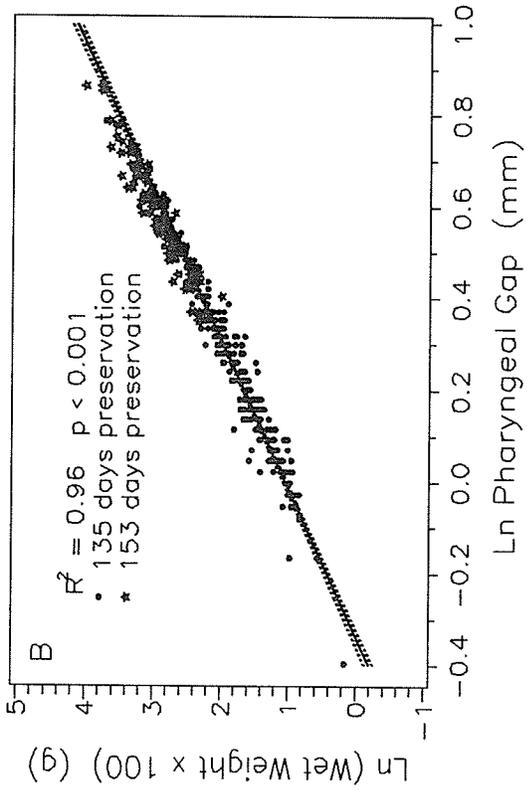
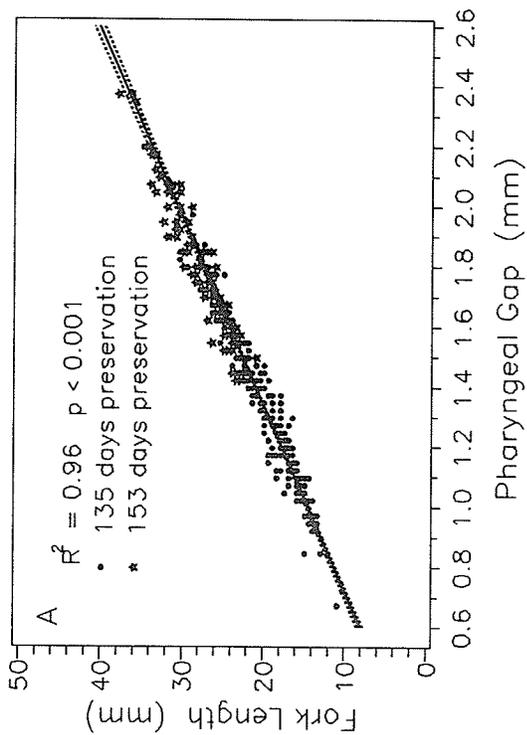
A number of physical and chemical measurements were made during each of the five sampling trips to Whitefish Lake in 1987. Measurements were taken at each of six seining locations visited during the midday sampling period (12:00 - 16:00). Sampling sites were approximately 25 m offshore and at a depth of about 3 m. A 23 cm diameter black and white patterned disc was used to estimate secchi depth (Wetzel 1983). Conductivity ($\mu\text{mho}\cdot\text{cm}^{-1}$, standardized to 25° C) was measured in surface water samples, using a Fisher Conductivity Meter, Model 152. Water samples were also collected in 300 ml glass-stoppered bottles for dissolved oxygen determination using the Winkler method (APHA 1985). Lastly, surface water temperatures were recorded with a YSI Instruments Tele-Thermometer. Results are presented in Table 1.

App. I, Table 1. Means (\pm 95 % CI) for estimates of secchi depth (m), conductivity ($\mu\text{mho}\cdot\text{cm}^{-1}$), dissolved O_2 ($\text{mg}\cdot\text{l}^{-1}$), and surface water temperature ($^{\circ}\text{C}$), made at seining locations in Whitefish Lake during each sampling period in 1987. Means are derived from six measures of each variable, except for June 3-4 sample, when $n=5$.

Sampling Dates	Secchi (m)	Conductivity ($\mu\text{mho}\cdot\text{cm}^{-1}$)	Diss. O_2 ($\text{mg}\cdot\text{l}^{-1}$)	Water Temp. ($^{\circ}\text{C}$)
June 2 - 4	1.8 \pm 0.19	288 \pm 20.6	9.6 \pm 0.66	13.4 \pm 1.37
June 22-23	2.6 \pm 0.48	317 \pm 21.4	8.6 \pm 0.42	20.8 \pm 0.78
July 14-15	2.8 \pm 0.25	n.m.	8.8 \pm 0.66	18.9 \pm 0.34
August 4	2.1 \pm 0.16	339 \pm 12.6	8.9 \pm 0.12	19.4 \pm 0.43
Sept. 22-23	1.9 \pm 0.20	324 \pm 17.0	10.0 \pm 0.16	14.95 \pm 0.40

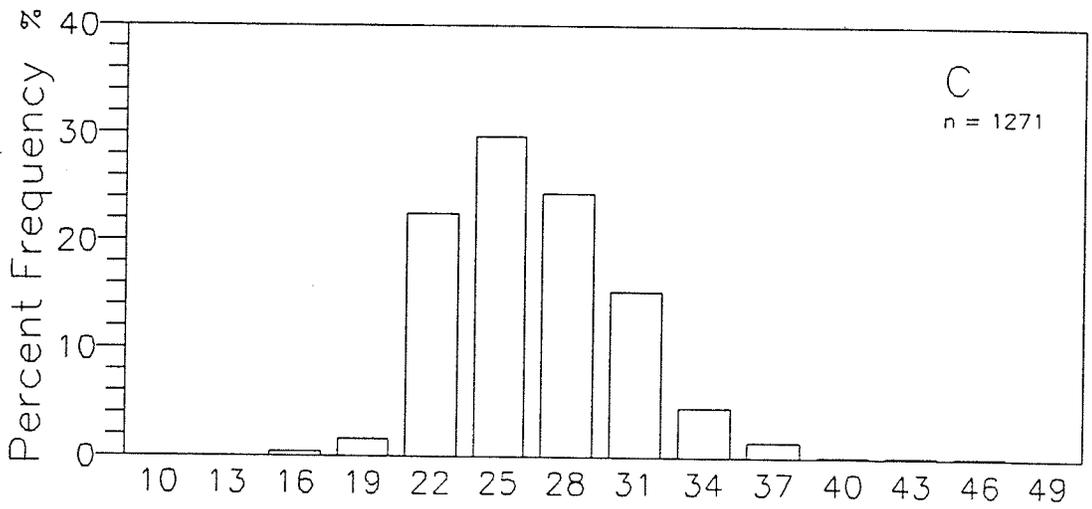
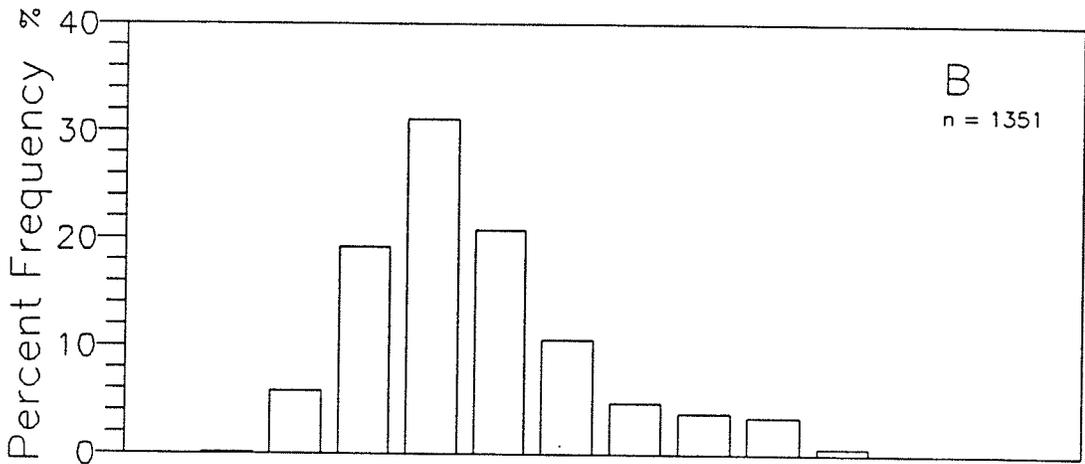
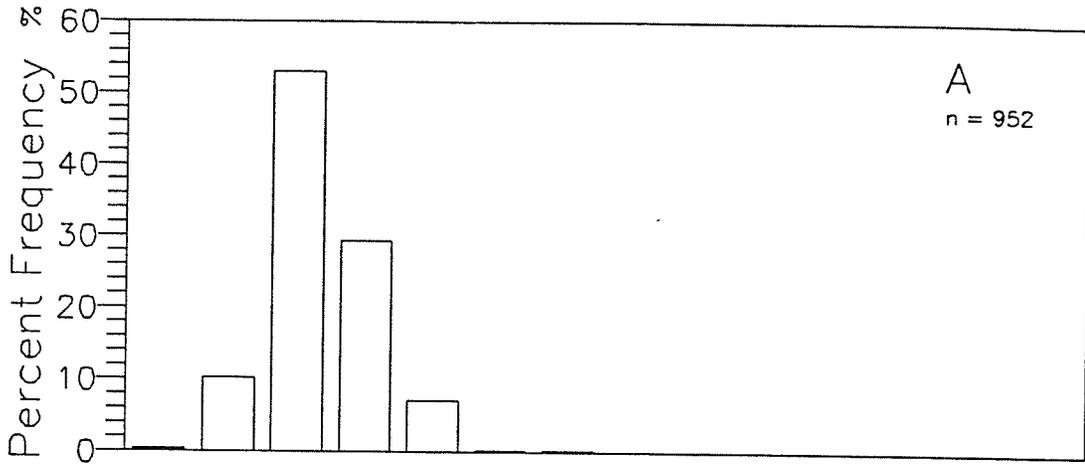
Appendix II

App. II, Figure 1. Regression lines and 95 % prediction limits for relationships of fork length (mm) to pharyngeal GAP (mm), and wet weight (g x 100) to pharyngeal GAP used in Chapter II. Wet weights were multiplied by 100 to prevent having negative logarithmic values. Plots are as follows: A). Fathead minnow fresh fork length versus pharyngeal GAP. B). Natural log (ln) of fathead minnow fresh weight (x 100) versus ln GAP. C). Spottail shiner fresh fork length versus GAP. D). Natural log (ln) of spottail shiner fresh weight (x 100) versus ln GAP.



Appendix III

App. III, Figure 1. Fork length frequency distributions (%) of forage fish used in each trial of the feeding experiment presented in Chapter III. Forage fish are pooled from all aquaria. A). Trial 1, July 3-4. B). Trial 2, July 21-22. C). Trial 3, August 14-15.



Fork Length (mm)

Appendix IV

Results of overall analyses of variance used in each trial of the feeding experiment are provided in this appendix. A blocked 2 x 2 factorial ANOVA was used for both measures in trials 1 and 2 (Tables 1 and 2). The SAS MODEL statement used in PROC GLM (SAS Institute Inc. 1985) for this ANOVA was:

variable = Day Species|Water Clarity.

A blocked split plot ANOVA was used for the third trial (Table 3) because light level was a significant factor. The model statement was:

**variable = Day Light Day*Light Clarity|Species Light*Clarity
Light*Species Light*Clarity*Species;**

and the TEST statement for testing light level effects against main plot error was:

TEST H = Light E = Day*Light.

F-values for block effects (day of experiment) are not presented in these ANOVA tables, because this source of variation was not of interest as long as block x treatment interactions were not significant, as was the case in all trials.

App. IV, Table 1A. ANOVA for differences in mean consumption (g forage fish / g predator body weight) in trial 1.

Source	df	Mean Square	F	probability > F
<u>Model</u>	4	0.0041	13.23	0.0001
Day	1	0.0049	-	-
Species	1	0.0076	24.52	0.0001 ***
Water Clarity	1	0.0022	7.14	0.0150 *
Species x Water Clarity	1	0.0017	5.44	0.0310 *
Error	19	0.00031		
Corrected Total	23			

Table 1B. ANOVA for differences in mean stomach fullness in trial 1.

Source	df	Mean Square	F	probability > F
<u>Model</u>	4	2.6669	9.03	0.0003
Day	1	1.8148	-	-
Species	1	6.5975	22.34	0.0001 ***
Water Clarity	1	0.0651	0.22	0.6440
Species x Water Clarity	1	2.1901	7.42	0.0130 *
Error	19	0.2953		
Corrected Total	23			

App. IV, Table 2A. ANOVA for differences in mean consumption (g forage fish / g predator body weight) in trial 2.

Source	df	Mean Square	F	probability > F
<u>Model</u>	4	0.0039	10.32	0.0001
Day	1	0.0011	-	-
Species	1	0.0067	17.42	0.0004 ***
Water Clarity	1	0.0054	14.23	0.0010 ***
Species x Water Clarity	1	0.0026	6.85	0.0150 *
Error	23	0.00038		
Corrected Total	27			

Table 2B. ANOVA for differences in mean stomach fullness in trial 2.

Source	df	Mean Square	F	probability > F
<u>Model</u>	4	3.4155	7.77	0.0004
Day	1	4.1481	-	-
Species	1	4.1915	9.53	0.0050 **
Water Clarity	1	3.8135	8.67	0.0070 **
Species x Water Clarity	1	1.5089	3.43	0.0770
Error	23	0.4398		
Corrected Total	27			

Table 3B. ANOVA for differences in mean stomach fullness in trial 3.

Source	df	Mean Square	F	probability > F
<u>Model</u>	9	2.1839	4.65	0.0016
Day	1	0.6096	-	-
Light Level	1	1.0940	0.85	0.5260
Main plot error	1	1.2867	-	-

Species	1	0.2658	0.57	0.4600
Water Clarity	1	5.7658	12.27	0.0020 **
Species x Water Clarity	1	4.5627	9.71	0.0050 **
Light Level x Species	1	0.0957	0.20	0.6560
Light Level x Water Clarity	1	4.8179	10.25	0.0040 **
Light Level x Species x Water Clarity	1	1.1565	2.46	0.1310
Error	22	0.4699		
Corrected Total	31			