THE WHITE PERCH AND ITS INTERACTION WITH YELLOW PERCH IN LAKE ERIE

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THE WHITE PERCH AND ITS INTERACTION WITH
YELLOW PERCH IN LAKE ERIE

DISSERTATION

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The Ohio State University
1988

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Professor F.J. Margraf, Adviser

White perch were first caught in Lake Erie in 1954. Since the mid-1970's, the white perch population has expanded rapidly, resulting in possible major interactions with the native yellow perch. In this study, I investigated these interspecific interactions by determining and comparing the consumption rates, diets, and individual apparent growth of white perch and yellow perch from field-collected data taken during 1983-85 and 1987. (Most of the yellow perch data were obtained from a separate project conducted by the Ohio Cooperative Fish and Wildlife Research Unit.) White perch generally had higher consumption rates than yellow perch and both species consumed more in the central than in the western basin. While yellow perch grew faster in the central basin, reflecting the greater consumption rates, white perch did not grow to the same extent. Perhaps white perch are better adapted to the thermal conditions of the western basin or are actually non-
discrete populations and therefore, growth differences cannot be detected. To calculate white perch consumption, I first determined their gastric evacuation rate \((R)\) from laboratory and diel field-collected data, resulting in the following temperature-dependent equation: \(R=0.028e^{0.106T}\). Diets were most similar in summer and less so in spring and autumn when yellow perch consumed more benthic organisms or fish. Of 68 diet overlap comparisons during a three-year period, 52% were significant (Schoener index > 0.6). I conducted zooplankton feeding selectivity experiments with YOY white perch and yellow perch in allopatry and sympatry. A total of 8 trials showed that both species were equally capable of feeding on the "natural mix" of Lake Erie zooplankton, with no differences in allopatry or sympatry in either species. Although some differences between species were detected by ANOVAs, these were not consistent throughout the trials. MANOVAs of the array of organisms eaten showed no differences for all trials. In the final part of this study, I performed in situ field-enclosure competition experiments with YOY white perch and yellow perch. Although the results are equivocal, two of the three trials showed negative relationships of fish growth as a function of fish density and white perch growth was not as affected by increased densities as was yellow perch.
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I would like to thank Paul Minnillo for his technical assistance. During many difficult times, his hard work and friendship kept me going.

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Department of Commerce, and from the State of Ohio. Additional funding was provided by the Ohio Cooperative Fish and Wildlife Research Unit, which is jointly supported by the U.S. Fish and Wildlife Service, the State of Ohio, and The Ohio State University.

Finally, I give into sentimentality by thanking my parents, Charles and Nellie Parrish, for their unending support and encouragement in helping me attain my goals. I am also thankful of my sister and her family: Doris, Dan, and Doug McPherson. And these acknowledgements would not be complete without expressing gratitude to Mrs. Effie Owens, my wonderful aunt, who has always been an inspiration to me and who shared with me the joy of fishing in her farm pond.
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PUBLICATIONS

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Academy of Science 61:92-95.

Electrofishing vs. angler harvest: Different length-
frequency distributions. Transactions of the Kentucky
Academy of Science 46(1-2):57.

Evaluation of a direct potentiometric method for sodium
and potassium use in the Du Pont 'aca'. Clinical Chemistry
29:1090-1092.
PRESENTATIONS

Parrish, D.L., and F.J. Margraf. Role of the exotic white perch in the Lake Erie fish community relative to the native yellow perch. 50th Midwest Fish and Wildlife Conference, Columbus, OH, 4-7 December 1988.


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LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, EUB=Eubosmina, and OST=Ostracods. N=number of fish.

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Preference values (Manly/Chesson index) for white perch (WP) and yellow perch (YP) from allopatric-sympatric feeding selectivity experiments in 1987. LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, CAL=calanoid copepods, EUB=Eubosmina, and BYT=Bythotrephes. Preferences > .20 in trials 1-3 and 5 and > .17 in trial 4 are underlined; indicating positive selection for a given prey. N=number of fish.

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GENERAL INTRODUCTION

Fisheries of Lake Erie are currently managed on an individual species basis. While this approach led to rehabilitation of the walleye (*Stizostedion vitreum vitreum*) fishery, it has resulted in only limited success for other species. For management to progress toward a more integrated, community approach, research is needed in areas involving interactions that influence Lake Erie fish communities: especially important is the white perch (*Morone americana*) and yellow perch (*Perca flavescens*) relationship.

Since the mid-1970's, white perch, an East Coast estuarine fish, has proliferated in Lake Erie, with both Ohio and Ontario showing large increases in young-of-the-year (hereafter YOY) and commercial catch abundances in the early-1980's (Tables 1 and 2). Boileau (1985) speculated that temperature preference and fecundity were principal among the factors affecting white perch ability to invade and colonize new areas. White perch are more apt to invade areas that reach a temperature of at least 24 C (Scott and Crossman 1979) and appear to find fairly eutrophic waters suitable habitat (Hurley and Christie 1977), making Lake Erie an ideal location for white perch. Also, white perch

1
Table 1. White perch YOY (young-of-the-year) abundance (number per trawling hour) in western Lake Erie, Ohio (Ohio Department of Natural Resources 1985) and Ontario (Ontario Ministry of Natural Resources 1984) districts.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ohio</th>
<th>Ontario</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>---</td>
<td>24</td>
</tr>
<tr>
<td>1981</td>
<td>---</td>
<td>112</td>
</tr>
<tr>
<td>1982</td>
<td>606</td>
<td>822</td>
</tr>
<tr>
<td>1983</td>
<td>276</td>
<td>831</td>
</tr>
<tr>
<td>1984</td>
<td>3360</td>
<td>15297</td>
</tr>
</tbody>
</table>

Table 2. Commercial fish landings (kg.) of white perch from western Lake Erie, Ohio (Ohio Department of Natural Resources 1985) and Ontario (Great Lakes Fishery Commission 1984) districts.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ohio</th>
<th>Ontario</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>&lt;454</td>
<td>----</td>
</tr>
<tr>
<td>1981</td>
<td>1361</td>
<td>----</td>
</tr>
<tr>
<td>1982</td>
<td>12247</td>
<td>3822</td>
</tr>
<tr>
<td>1983</td>
<td>50802</td>
<td>46131</td>
</tr>
<tr>
<td>1984</td>
<td>59421</td>
<td>594706</td>
</tr>
</tbody>
</table>
have a high fecundity rate (Sheri and Powers 1968) which allows for rapid colonization of an appropriate resource.

In the absence of predators, white perch populations frequently expand beyond the capacity of the food resource to support them and they become stunted. In the Bay of Quinte, Hurley and Christie (1977) correlated the white perch expansion with the decline in predators, along with increased eutrophication. Busch et al. (1977) and Nepszy (1977) thus predicted that white perch would not become a dominant species in Lake Erie because of the presence of piscivorous species (i.e., walleye and white bass, *Morone chrysops*). However, piscivory has not controlled the white perch in Lake Erie and the population continues to expand at a rapid rate. Knight et al. (1984) found that Lake Erie walleyes ate clupeids and shiners almost exclusively when abundant and generally resorted to consumption of spiny-rayed fish only when soft-rayed fish were unavailable. So, even though walleyes may consume some white perch, the probability of walleye predation controlling the white perch population is doubtful.

Schaeffer (1984) and Schaeffer and Margraf (1986a,b; 1987) studied white perch distributional patterns, population dynamics, and food habits during the initial period of proliferation in the Sandusky Bay area of western Lake Erie. They concluded that white perch interact with walleyes, white bass, and yellow perch, resulting in
suspected intense predatory and competitive reactions. White perch prey on walleye eggs, use the same food resources as yellow perch, and use the same spawning grounds as white bass (resulting in some hybridization).

Of the three interspecific interactions, investigating white perch-yellow perch competition is most imperative. Not only is the indigenous yellow perch of major importance in Lake Erie as both a commercial and a sport species, it has experienced reduced growth rates since 1970 resulting from limited food resources (Hayward and Margraf 1987). While Schaeffer and Margraf (1986a) provide some preliminary evidence, they fall short of proving that white perch negatively interact with yellow perch because of non-overlapping collecting sites and times, and a sampling regime restricted to the Sandusky Bay area of western Lake Erie. Thus any impacts of white perch competition with other species need to be quantified for a broader area of the Lake and during a period of several years.

Since the invasion, white perch and yellow perch have been caught in the same trawl hauls in Lake Erie (Table 3) and in the same gill nets in Lake Ontario (Elrod et al. 1981). In Lake Ontario, age-1 and older white perch and similar-sized yellow perch not only share the same space but also, consume the same food types (Elrod et al. 1981). Schaeffer and Margraf (1986a) noted high diet overlaps between Lake Erie white perch and yellow perch, especially
Table 3. Summer survey of YOY (young-of-the-year) yellow perch and white perch (number per trawling hour) from 1980-86 at East Harbor in Lake Erie's western basin (USFWS-Sandusky, Ohio 1987).

<table>
<thead>
<tr>
<th>Year</th>
<th>Yellow Perch</th>
<th>White Perch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>105</td>
<td>2</td>
</tr>
<tr>
<td>1981</td>
<td>76</td>
<td>173</td>
</tr>
<tr>
<td>1982</td>
<td>1456</td>
<td>925</td>
</tr>
<tr>
<td>1983</td>
<td>20</td>
<td>652</td>
</tr>
<tr>
<td>1984</td>
<td>29</td>
<td>7049</td>
</tr>
<tr>
<td>1985</td>
<td>42</td>
<td>2607</td>
</tr>
<tr>
<td>1986</td>
<td>1295</td>
<td>8349</td>
</tr>
</tbody>
</table>
during June and July, but a divergence in diets occurred in August and September when zooplankton prey availability was lowest. In this case, significant diet overlap is not an indicator of competition (Abrams 1980; Schoener 1982; MacNally 1983), but rather, the high diet overlap followed by a divergence in diets may imply that these populations compete by contributing to the decline in zooplankton abundance through overgrazing. Therefore, the most intense competition would occur at the point of divergence, which is presumably correlated with the zooplankton decline.

Hanson and Leggett (1985) and Werner (1986) describe several conditions, especially related to fish communities, which tend to indicate the occurrence of competitive interactions. For example, if the individual growth rates of an indigenous species decline after the invasion of a new species and both species use the same food-limiting resource, then competition has presumably occurred (Sale 1979; Connell 1983). The reactions of species involved could be manifested in decreased individual growth rates because of less available prey or divergence to less desirable prey. Likewise, the invasion of white perch into Lake Erie has evidently resulted in competitive interactions with the native yellow perch population. Even though yellow perch growth rates have been declining for 20 years, a more rapid decline has occurred since the white perch invasion and yellow perch growth rates in the more
food-limited western basin have declined even more than in
the central basin (Fig.1). During the period of their rapid
expansion, individual white perch in Lake Erie were growing
at rates approaching the fastest known for any population
(Schaeffer and Margraf 1986b).

Also, an indication of competition would be decreased
growth rate of the native species, manifested at the
population level by decreased density or biomass as the
invading species increases. In the Bay of Quinte, yellow
perch density did not change during the increase in white
perch density (Hurley and Christie 1977). As a likely
explanation of this, food supply was ample to support the
increase in overall fish density. This scenario is unlikely
in Lake Erie because food is limited, and thus, it is
suspected that yellow perch densities have decreased in
recent years. Hanson and Leggett (1982) found that total
fish biomass (irrespective of species numbers) was strongly
correlated to macrobenthos biomass. If this be the case in
Lake Erie, yellow perch population biomass had to decrease
either through a reduction in the number of individuals or a
decline in individual growth rates.

This study is composed of four basic parts. First, I
adopted the approach of using extensive field-collected fish
to document the current status of consumption, diet, and
apparent growth in both white perch and yellow perch. (Most
of the data shown for yellow perch were obtained from a
Figure 1. Mean total lengths of age-2+ yellow perch in October from the central and western basins of Lake Erie (1970-85). White perch are shown to appear in 1975 (Ohio Department of Natural Resources data).
YELLOW PERCH
MEAN LENGTHS IN OCTOBER

White Perch Present

CENTRAL BASIN

WESTERN BASIN

YEAR

MEAN TOTAL LENGTH (mm)

150

160

170

180

190

200

210

220

230

(ODNR)
separate project (Hayward 1988) at the Ohio Cooperative Fish and Wildlife Research Unit.) Also, before white perch consumption could be calculated, it was necessary to perform laboratory gut-evacuation experiments, since that information had not been previously determined. Third, I performed zooplankton feeding selectivity experiments with YOY white perch and yellow perch in allopatry and sympatry. These experiments were performed to assess the feeding capabilities of YOY of both species and to determine if feeding patterns were altered in the sympatric condition resulting from either interference or exploitative competition. Finally, in 1986 and 1987 I conducted in situ field-enclosure competition experiments using YOY white perch and yellow perch.
Chapter 1
Consumption, diet, and apparent growth of white perch compared to those of yellow perch

Introduction

I investigated white perch-yellow perch interactions by determining consumption rates, examining diets and apparent growth of white perch, and comparing these data to those of yellow perch. Knowledge of not only the prey type, but also the amount of prey eaten is important in determining the degree of interaction and resource partitioning. Because diet overlap information alone is not sufficient evidence of competition, I also determined individual apparent growth of white perch in the central and western basins of Lake Erie and compared them to those of concomitantly caught yellow perch.
Methods

Lake Erie white perch and yellow perch were collected, frozen, and archived in 1983, 1984, and 1985 by the Ohio Division of Wildlife and the Ohio Cooperative Fish and Wildlife Research Unit. The collections were from bi-weekly bottom trawls occurring from May to November at a series of stations in the central and western basins (Fig. 2). Occasionally, gill net sets supplemented the trawl collections. Also used were samples from 1983 and 1984 diel trawl collections. Diel samples were taken from one western basin site (near Middle Sister Island) and one central basin site (off Fairport, Ohio) three times during the collecting season, usually May, July, and September. Diel trawling consisted of bottom collections every 3-h for a 24-h period. In 1987, diel trawling was done in May and July at a site in the western basin (near Green Island) aboard the OSU Biolab.

All 1983-85 white perch and yellow perch from each trawl or gill net collection were labeled with date, location, and time of capture, and placed on dry ice to deter digestion or regurgitation of stomach contents. The 1987 fish were immediately placed on ice and then transferred to the laboratory freezer within one hour of collection. In the laboratory, white perch were sexed, weighed (g), measured (SL and TL, mm) and scale samples taken for aging. Stomach and intestinal contents were both
Figure 2. Lake Erie and the four central basin and six western basin bottom trawling sites where white perch and yellow perch were sampled in 1983-85.
LAKE ERIE

SAMPLING SITES

1. FAIRPORT
2. CLEVELAND
3. LORAIN
4. VERMILION
5. CEDAR POINT
6. EAST HARBOR
7. KELLEYS
8. GREEN ISLAND
9. BONO
10. MIDDLE SISTER
wet-weighed and dry-weighed for 24-h at 80 C. (Yellow perch collected in 1983-85 were processed similarly in a separate project at the Ohio Cooperative Fish and Wildlife Research Unit.) Fish showing evidence of regurgitation were not used to determine food consumption.

Amounts of food in individual stomachs from each of the successive trawl hauls were first determined to estimate quantities of food consumed over 24-h periods during diel sampling. The amount of food in a stomach was expressed as the ratio of total weight of food material to weight of the fish (weight-specific food quantity). Medians (and quartiles) of weight-specific food quantities (g/g) were determined from each of the successive trawl collections. Because of low numbers of white perch in many of the trawls, fish were pooled over a single size-range of 85-200 mm. Point estimates (at 3-h intervals) of median food amounts in stomachs (g/g) were converted to daily consumption rates (g/g/d) using the exponential algorithm of Elliot and Persson (1978). Instantaneous rates of gastric evacuation for white perch were estimated from laboratory gastric evacuation experiments and diel field-collected data (see Chapter 2).

I was also able to estimate daily food consumption (g/g/d) for white perch from single trawl hauls made from 0800 to 2000 hours following the correlative method used by Hayward and Margraf (1987). In this method, median weight-
specific food quantities from these peak feeding hours were multiplied by my white perch temperature-dependent gastric evacuation rate (R) and then regressed against calculated diel consumption rates. From those collections made from 0800 to 2000 hours, five regression relationships were derived (Fig. 3). The $r^2$ values obtained by Hayward and Margraf (1987) for yellow perch compared well with those at 1100, 1400, 1700 hours ($r^2$ = 0.87, 0.84, 0.91). Single trawl (g/g) values were then converted to consumption (g/g/d) by using the regression from the nearest time to that of the actual trawling time. As with the yellow perch, white perch were sometimes absent from the summer diel trawls and therefore, the correlative method was used to estimate food consumption for the 24-h period.

White perch consumption rates were compared between basins to determine if white perch were experiencing similar interbasin differences in feeding conditions as yellow perch (Hayward and Margraf 1987). Subsequently, white perch and yellow perch consumption rates were compared for both basins.

White perch stomach contents were identified to the same taxonomic level as were those of yellow perch, with 1983 being a more cursory treatment, and 1984 and 1985 being much more detailed (Hayward et al. 1985). In 1983 white perch, food items were identified to only family level in some cases and diet composition was expressed as percent
Figure 3. Regressions of temperature adjusted median weight-specific food ratios against calculated 24-h diel consumption rates from 1983-84. Times range from 0800 to 2000 hours.
frequency of occurrence. The 1984 and 1985 white perch stomach contents were identified in most cases to the genus level and individual food items were measured. In 1987, both species stomach contents were identified generally to the genus level. Percent diet composition was then determined using accepted length-weight regressions of the available prey, which included zooplankton, benthic organisms, and fish species (P.K. Cunningham and G.G. Mittelbach, personal communication). Means of prey sizes consumed in 1984-85 were used in the regressions for the 1983 fish. Diet overlap for concomitantly caught fish, on the basis of size of food and taxonomic composition, were determined using the Schoener (1970) index. Because of the sparse consumption of fish by both species, all fish species were lumped into a single category for purposes of calculating the Schoener index.

White perch in excess of 15 individuals from trawl collections (n>15), were reserved as growth-only fish. These fish were sexed, aged from scale samples, measured (SL and TL, mm) and whole specimen wet-weights and dry-weights were determined. Dry-weights were obtained after specimens were dried for 72-h at 80 C and used to derive a dry-wet weight regression. White perch individual apparent growth rates were compared on an interbasin basis, then white perch and yellow perch apparent growth rates were compared for both basins.
Results

Interbasin differences in white perch weight-specific food percentages \((g/g \cdot 100)\) are apparent from 1983-84 diel samplings (Figs. 4-7). In spring and autumn 1983, the amount of food in stomachs of central basin white perch exceeded that of those in the western basin with the exception of one time period. Also in 1983, summer and autumn food amounts in central basin white perch were high compared to other times and to yellow perch. The spring 1984 diel patterns for the two basins are the most similar of the 1983-84 diels.

Comparing white perch and yellow perch feeding levels, in spring 1987 in the western basin, white perch food amounts were considerably higher than those of yellow perch at all times during the 24-h period (Fig. 8). Because of increased food evacuation at high temperatures in the summer 1987 diel (Fig. 9), the curves are very similar except during times of higher feeding (0800-1400).

White perch (85-205 mm) consumption rates for 1983-84 and 1987 diels are shown, along with yellow perch values from 1983 (85-139 mm) and 1987 (85-205 mm) (Table 4). Generally, white perch consumption rates are higher in the central basin than in the western; a pattern similar to yellow perch. Also, when examining differences in consumption rates (white perch \((g/g/d)\)-yellow perch \((g/g/d)\))
Figure 4. Medians and quartiles of weight-specific food percentages (food weight/body weight$^{-1}$.100) for diel-sampled white perch (85-205 mm) from the central and western basins of Lake Erie in spring 1983.
Figure 5. Medians and quartiles of weight-specific food percentages (food weight · body weight⁻¹ · 100) for diel-sampled white perch (85-205 mm) from the central basin of Lake Erie in summer 1983.
Figure 6. Medians and quartiles of weight-specific food percentages (food weight·body weight $^{-1}$·100) for diel-sampled white perch (85-205 mm) from the central and western basins of Lake Erie in autumn 1983.
Figure 7. Medians and quartiles of weight-specific food percentages (food weight\·body weight\(^{-1}\)\·100) for sampled white perch (85–205 mm) from the central and western basins of Lake Erie in spring 1984.
Figure 8. Medians and quartiles of weight-specific food percentages (food weight·body weight$^{-1}$·100) for diel-sampled white perch and yellow perch (85-205 mm) from the western basin of Lake Erie in spring 1987.
Figure 9. Medians and quartiles of weight-specific food percentages (food weight/ body weight$^{-1} \cdot 100$) for diel-sampled white perch and yellow perch (85-205 mm) from the western basin of Lake Erie in summer 1987.
Table 4. White perch (85-205 mm) and yellow perch (85-139 mm) consumption rates for 1983-84 diel samples from the western and central basins and in 1987 from the western basin of Lake Erie. In two western basin diels, too few white perch were caught to calculate consumption rates. Yellow perch values for 1983 are from Hayward and Margraf (1987).

<table>
<thead>
<tr>
<th>Season/Year</th>
<th>White Perch</th>
<th>Yellow Perch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western</td>
<td>Central</td>
</tr>
<tr>
<td>Spring 1983</td>
<td>0.032</td>
<td>0.052</td>
</tr>
<tr>
<td>Summer 1983</td>
<td>------</td>
<td>0.219</td>
</tr>
<tr>
<td>Autumn 1983</td>
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<tr>
<td>Spring 1984</td>
<td>0.026</td>
<td>0.026</td>
</tr>
<tr>
<td>Summer 1984</td>
<td>0.097</td>
<td>0.121(^a)</td>
</tr>
<tr>
<td>Autumn 1984</td>
<td>------</td>
<td>0.052(^a)</td>
</tr>
<tr>
<td>Spring 1987</td>
<td>0.068</td>
<td></td>
</tr>
<tr>
<td>Summer 1987</td>
<td>0.074</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Consumption rate calculated from correlation regression.
\(^b\)See Hayward (1988).
on a diel basis, the white perch values are usually higher (Fig.10).

Consumption rate differences between species were calculated from single bi-weekly trawl values (1983-85) using the correlative method. Medians (Fig.11), upper quartiles (Fig.12), and lower quartiles (Fig.13) corroborate the previously shown diel patterns of white perch-yellow perch consumption rate differences; white perch consumption usually exceeds that of yellow perch throughout the sampling season.

Diets of Lake Erie white perch (85-205 mm) from six western basin and four central basin sites from 1983-85 are summarized (Figs.14-29). Each pie graph represents the stomach contents of fish caught in a single trawl and a minimum of three fish in the sample. Spring samples correspond to May-June, summer samples to July-August, and autumn samples to September-November. A maximum of three trawls throughout the sampling season are shown for a site; with the exception of Middle Sister in 1984, where four are shown (Fig.18). Organisms in each pie graph are expressed as percent biomass calculated from length-weight regressions of the prey. Only organisms that comprised 1% or more are shown on the graph. Therefore, total percent biomass of the graphs range from 98 to 100%. Fish species are labeled by species name if only one species was eaten and identifiable.
Figure 10. Differences in white perch and yellow perch consumption rates (g/g/d) calculated from spring (SP), summer (SU), and autumn (AU) diel sampling in the central and western basins of Lake Erie in 1983-84 and in the western basin in 1987.
Figure 11. Differences in median values of white perch and yellow perch consumption rates (g/g/d) calculated with the correlate method using single-trawl data throughout the 1983-85 sampling seasons.
Figure 12. Differences in upper quartile values of white perch and yellow perch consumption rates (g/g/d) calculated with the correlate method using single-trawl data throughout the 1983-85 sampling seasons.
Figure 13. Differences in lower quartile values of white perch and yellow perch consumption rates (g/g/d) calculated with the correlate method using single-trawl data throughout the 1983-85 sampling seasons.
Figure 14. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and summer 1983 at Middle Sister.
Middle Sister

1983

Spring

- Chironomidae 75%
- Ostracode 1%
- Eubosmina 4%
- Daphnia 1%
- Cyclopoid 5%
- Chydorid 12%

Diet Overlap = 0.78

Summer

- Chironomidae 20%
- Chydorid 1%
- Daphnia 46%
- Eubosmina 1%
- Leptodora 33%

- Daphnia 13%
- Chironomidae 26%
- Leptodora 43%
- Eubosmina 1%
- Fish 2%

Diet Overlap = 0.66

White Perch

Yellow Perch
Figure 15. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and autumn 1983 at East Harbor.
East Harbor

1983

Spring

- Cyclopoid 3%
- Chyadorid 1%
- Chironomidae 20%
- Daphnia 43%
- Eubosmina 1%
- Leptodora 32%

Diet Overlap = 0.80

Autumn

- Daphnia 78%
- Cyclopoid 7%
- Chyadorid 1%
- Chironomidae 8%
- Amphipoda 2%
- Leptodora 3%

Diet Overlap = 0.15

White Perch

Yellow Perch
Figure 16. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring 1983 at Vermilion and Lorain.
Vermilion
1983

Diet Overlap = 0.63

Lorain
1983

Diet Overlap = 0.96
Figure 17. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and autumn 1983 at Fairport.
Fairport
1983

Spring

Chironomidae 85%
Isopoda 12%
Cyclopoid 2%
Chydorid 1%

Diet Overlap = 0.85

Autumn

Chironomidae 69%
Oligochaeta 2%
Nematoda 2%
Isopoda 16%
Sidae 1%
Hirudinea 3%
Daphnia 6%

Cyclopoid 3%

Chironomidae 48%
Leptodora 32%
Sidae 10%
Sphaeridae 7%

Diet Overlap = 0.49

White Perch

Yellow Perch
Figure 18. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring, summer, and autumn 1984 at Middle Sister.
Middle Sister

1984

Spring
- Copepod 16%
- Chironomidae 20%
- Ostracode 2%
- Chironomidae 15%
- Copepod 19%
- Ostracode 21%
- Haploplecton 1%
- Other taxa 3%
- Copepod 10%
- Ostracode 9%

Diet Overlap = 0.73

Summer-1
- Daphnia 98%
- Leptodora 2%
- Daphnia 41%
- Leptodora 13%

Diet Overlap = 0.44

Summer-2
- Daphnia 72%
- Leptodora 16%
- Fish 12%
- Leptodora 16%
- Fish 27%

Diet Overlap = 0.81

Autumn
- Copepod 2%
- Chironomidae 33%
- Ostracode 2%
- Copepod 29%
- Copepod 29%
- Ostracode 1%
- Fish 10%

Diet Overlap = 0.37

White Perch

Yellow Perch
Figure 19. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring 1984 at Cedar Point and in the summer and autumn 1984 at Bono.
Cedar Point 1984

Spring
- Daphnia 44%
- Eubosmina 2%
- Leptodora 44%

Diet Overlap = 0.62

Bono 1984

Summer
- Daphnia 96%
- Fish 4%

Diet Overlap = 0.76

Autumn
- Daphnia 16%
- Leptodora 8%
- Chironomidae 20%
- Fish 56%

Diet Overlap = 0.53

White Perch

Yellow Perch
Figure 20. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and summer 1984 at Green.
East Harbor
1984

Autumn
Chironomidae 67%
Leptodora 11%
Hydracarina 6%
Eubosmina 10%
Cyclopoid 3%
Daphnia 3%
Chironomidae 43%
Leptodora 11%
White Perch 17%
Fish 31%
Smelt 2%
Diet Overlap = 0.50

Green
1984

Spring
Daphnia 87%
Chironomidae 12%
Leptodora 1%
Chironomidae 70%
Fish 1%
Daphnia 28%
Diet Overlap = 0.40

Summer
Daphnia 68%
Chironomidae 1%
Fish 31%
Daphnia 22%
Chironomidae 6%
Hydracarina 3%
Fish 68%
Diet Overlap = 0.54

White Perch
Yellow Perch
Figure 21. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring, summer, and autumn 1984 at Kelles.
Diet Overlap = 0.64

Diet Overlap = 0.85

Diet Overlap = 0.54

White Perch

Yellow Perch
Figure 22. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring, summer, and autumn 1984 at Vermilion.
Vermilion

1984

Spring

Daphnia 94%

Diet Overlap = 0.54

Summer

Daphnia 100%

Diet Overlap = 0.56

Autumn

Daphnia 71%

Diet Overlap = 0.86

White Perch

Yellow Perch
Figure 23. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the autumn 1984 at Cleveland and in the spring and autumn 1984 at Lorain.
Cleveland
1984

Autumn

Chyadorid 55%
Chironomidae 8%
Eubosmina 21%
Cyclopoid 8%
Daphnia 8%

Diet Overlap = 0.66

Lorain
1984

Spring

Chyadorid 2%
Cyclopoid 5%
Daphnia 14%
Hydracarina 4%
Isopoda 40%
Nematoda 2%

Diet Overlap = 0.46

Autumn

Daphnia 80%
Chironomidae 2%
Smelt 18%

Diet Overlap = 0.94

White Perch

Yellow Perch
Figure 24. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring, summer, and autumn 1984 at Fairport.
Spring

- Chironomidae: 86%
- Isopoda: 6%
- Hirudinea: 1%
- Eubosmina: 1%
- Cyclopoid: 4%
- Calanoid: 1%

Diet Overlap = 0.75

Summer

- Daphnia: 89%
- Chironomidae: 10%
- Leptodora: 1%

Diet Overlap = 0.91

Autumn

- Chyadorid: 46%
- Chironomidae: 10%
- Amphipoda: 26%
- Daphnia: 4%
- Eubosmina: 2%
- Hirudinea: 1%
- Isopoda: 8%
- Skladae: 2%
- Leptodora: 1%

Diet Overlap = 0.28

White Perch

Yellow Perch
Figure 25. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the autumn 1985 at Middle Sister and in the spring and summer 1985 at Kelleys.
Middle Sister 1985

Diet Overlap = 0.53

Kelleys 1985

Diet Overlap = 0.96

Diet Overlap = 0.12
Figure 26. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and summer 1985 at Cedar Point and in the summer 1985 at Bono.
**Cedar Point**

1985

Diagram showing diet overlap:
- Spring: Diet Overlap = 0.82
- Summer: Diet Overlap = 0.64

**Bono**

1985

Diagram showing diet overlap:
- Summer: Diet Overlap = 0.43

**White Perch**

**Yellow Perch**
Figure 27. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the spring and summer 1985 at Vermilion.
Vermilion
1985

Spring
- Daphnia 96%
- Cyclopoid 1%
- Chironomidae 3%

Chironomidae
- 92%
- Ostracoda 1%
- Fish 3%
- Daphnia 3%

Diet Overlap = 0.07

Summer
- Chironomidae 44%
- Cyclopoid 16%
- Copepods 15%
- Daphnia 21%

Chironomidae
- 80%
- Daphnia 8%
- Cyclopoid 1%
- Chydoridae 11%

Diet Overlap = 0.52

White Perch
Yellow Perch
Figure 28. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the autumn 1985 at Cleveland and in the spring and summer 1985 at Lorain.
1. Cleveland 1985

Autumn

Chyadorid 95%

Diet Overlap = 0.37

Lorain 1985

Spring

Chironomidae 96%

Diet Overlap = 0.96

Summer

Chironomidae 69%

Chyadorid 18%

Diet Overlap = 0.69

White Perch

Yellow Perch
Figure 29. Diets (percent biomass) of white perch and yellow perch and their diet overlap values from collections in the summer and autumn 1985 at Fairport.
Diet Overlap = 0.39

Diet Overlap = 0.71
Otherwise, the label "Fish" may represent a few species or unidentifiable fish.

Although the diet information is massive and somewhat complex, several trends can be noted. White perch feed on a large number of organisms. For example, at Fairport in the autumn 1983, 18 different taxa were consumed, although only 7 of those taxa were present at 1% or more (Fig.17). The broader diets are more apparent when white perch are eating mostly from the benthos rather than feeding on zooplankton. Seasonally, they feed more heavily on benthic organisms such as Chironomids in the spring, but switch to a more zooplanktivorous diet during the summer. The autumn is much more difficult to characterize because both benthos and zooplankton are eaten.

In addition to the Chironomids, other benthic organisms consumed belong to the following groups: Amphipoda, Hirudinea, Hydracarina, Isopoda, Nematoda, Oligochaeta, and Ostracoda. Generally, these prey are consumed to a lesser extent than the Chironomids, with a few notable exceptions (Nematoda at Middle Sister in Autumn 1984, Fig.18; Isopoda at Lorain in Spring 1984, Fig.23).

The majority of the zooplankton prey are the Cladocerans: Daphnia, Leptodora, and the Chydorids; and cyclopoid and calanoid copepods. Daphnia are major diet components at many of the sites during the summer season. The Cladoceran, Eubosmina, is a fairly ubiquitous organism
of the white perch diet, but is never found to be a large component at any time.

Following benthos and zooplankton, fish are eaten on occasion. It is obvious that white perch are rarely strictly piscivores, but rather opportunistic predators. No fish were eaten by white perch in 1983 (Figs.14-17). However, in 1984, fish were considered a significant component of the white perch diet (Fig.18-21, 23). Fish were present in the diets of white perch collected at all of the six western basin sites at least once throughout the 1984 season. Of the central basin stations, only the white perch collected at Lorain in the autumn had eaten fish. In 1985, only white perch collected during the summer at the western basin sites of Cedar Point and Kelleys ate fish. Many of the fish found in the white perch stomachs were unidentified. Of those that were identifiable, smelt (Osmerus mordax), Morone sp., and gizzard shad (Dorosoma cepedianum) were the most abundant.

As indicated by many of the high diet overlap values, yellow perch and white perch consume a major proportion of the same prey items (Figs.14-29). The diet overlaps were significant (>0.6) in 25 of the 48 comparisons (0.52). Some of the most frequent deviations from a significant overlap occurred when yellow perch were eating more benthos than white perch (e.g., East Harbor Autumn 1983, Fig.15; Green Spring 1984, Fig.20; Vermilion Spring 1984, Fig.22; Kelleys
Deviations can also be attributed to a greater occurrence of piscivory by yellow perch (e.g., East Harbor Autumn 1983, Fig.15; Fairport Autumn 1983, Fig. 17; Middle Sister Summer-1 and Autumn 1984, Fig.18; East Harbor Autumn 1984, Fig. 20; Green Summer 1984, Fig. 20; Kelleys Autumn 1984, Fairport Autumn 1984, Fig.24; and Cleveland Autumn 1985, Fig. 28).

Diet overlap values throughout the sampling season differed among sampling years (Fig.30). By years, the percent occurrence of significant diet overlaps in descending order were 1983, 1984, and 1985. On a seasonal basis, the lowest values were in the spring and autumn.

Additionally, I examined the possibility that differences in white perch and yellow perch sizes used in the calculations were responsible for the low overlap values. However, narrowing the size ranges did not result in an increase in significant diet overlap.

Diet items from white perch and yellow perch collected during the two 1987 diels are reported as percent occurrence (Fig.31). Only organisms with an occurrence of 5% or more are shown. In all prey categories, white perch consumed a greater number of organisms than yellow perch. The previously shown higher consumption data for these same white perch and yellow perch corroborate these findings.
Figure 30. Schoeners diet overlap index values from collections throughout the sampling seasons (May-October 1983-85).
Figure 31. Diets (percent occurrence) of white perch and yellow perch from 1987 diel sampling in May and July off Green Island in the western basin.
Also, from the 1987 diels, I calculated diet overlap for each sampling time during the two 24-h periods (Fig. 32). The values are significant during all active feeding times, except at 1400 and 1700h in July. Even at these times, the overlaps are approximately 0.5.

Determination of accurate growth patterns of western and central basin white perch according to back-calculations from the growth fish collections were essentially impossible (Table 5). The overwhelming majority of the fish caught were ages-1 and -2 for all three of the collecting years. Also, an intermittent sparsity of fish from many of the collecting stations, resulted in the inability to make comparisons across all stations. Therefore, white perch collected at Middle Sister and Kelleys were pooled as the western basin samples and all of the central basin sites were pooled. The interbasin differences in white perch total lengths at back-calculated ages-2 and -3, was not significant for the three year period (ANOVA, P > 0.05). Also, age-1 interbasin differences were not significant within the single years, but were significantly different (P < 0.001) across the three year period. There was a slight decline in length at the first annulus over the three year period.

White perch total lengths at age from all fish collected in October 1983-84 are shown with previously reported western basin data (Schaeffer and Margraf 1986b)
Figure 32. Schoener's diet overlap index values at 3-h intervals throughout 24-h sampling in May and July 1987 off Green Island in the western basin.
Table 5. Back-calculated total lengths (mm) of central basin (CB) and western basin (WB) white perch from 1983-85. Central basin fish are from all four collecting sites. Western basin fish are from Middle Sister and Kelleys.

<table>
<thead>
<tr>
<th>Year</th>
<th>Basin</th>
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<tbody>
<tr>
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<td>CB</td>
<td>85.1</td>
<td>148.9</td>
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<td></td>
<td>WB</td>
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<tr>
<td>1985</td>
<td>CB</td>
<td>79.5</td>
<td>---</td>
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</tr>
<tr>
<td></td>
<td>WB</td>
<td>80.5</td>
<td>152.5</td>
<td>185.9</td>
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</table>
(Fig. 33). From these results, we may presume there is a trend toward slower individual growth rates from 1981 to 1984 for the age-2+ and age-3+ fish. Even the age-1+ fish show a decrease from 1981-82, but the age-0+ have not declined. This is a discrepancy when compared to the back-calculation data. A potential problem encountered in comparing my results with those of Schaeffer and Margraf (1986b) is the dissimilar sampling sites; they used fish from Sandusky Bay. The back-calculation data also provide evidence that white perch do not experience large differences in individual growth attributable to interbasin collecting location.

I also examined differences in white perch apparent growth throughout a single season (1983). Interbasin differences in growth based on wet weights (g) of age-1 and -2 white perch, from the four central basin sites and one western basin site, are not detectable (Fig. 34). According to comparisons of seasonal growth rates of white perch, based on slopes of the wet weight regressions, central basin fish were growing faster than those in the western basin 3 of the 5 times (Table 6).

In contrast to white perch, data for yellow perch (Fig. 35, Hayward and Margraf 1987), show large interbasin differences in growth at ages-2 and -3. Unfortunately, 3-year-old white perch were not collected in large enough numbers in 1983 to make any comparisons.
Figure 33. Mean total lengths (mm) of white perch in the western basin of Lake Erie in 1981-82 (Schaeffer and Margraf 1986b) and from the central and western basins in 1983-84.
Figure 34. Mean wet weights (g) of age-1 and -2 white perch from four central basin sites and one western basin site throughout the sampling season in 1983.
Table 6. Linear regression slopes of seasonal growth according to mean wet weight (g) for individual year-classes in the western and central basins during 1983-85.

<table>
<thead>
<tr>
<th>Year-Class</th>
<th>Western Basin</th>
<th>Central Basin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981</td>
<td>0.347</td>
<td>-</td>
</tr>
<tr>
<td>1982</td>
<td>0.269</td>
<td>0.341</td>
</tr>
<tr>
<td>1983</td>
<td>-</td>
<td>0.295</td>
</tr>
<tr>
<td>1984</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 35. Mean wet weights (g) of age-1, -2, and -3 yellow perch from four central basin sites and two western basin sites throughout the sampling season in 1983 (Hayward and Margraf 1987).
Discussion

This is the first study in which white perch daily ration has been determined. Therefore, no comparisons can be made to white perch food consumption in other systems.

White perch from the central basin generally ate more than those from the western basin. This is a pattern similar to that exhibited by larger yellow perch (140-205 mm) and to a lesser degree, small yellow perch (85-139 mm) in 1983 (Hayward and Margraf 1987). The 1984 small yellow perch data, unavailable for presentation here, also show large interbasin differences in the summer and autumn diels (R. Hayward, personal communication).

When compared to yellow perch, white perch consumption rates were considerably higher. In 1983, yellow perch consumption ranged from 1.7% to 9.6% body weight, while white perch ranged from 3.2% to 21.9%. These comparisons were made between species of unequal size distributions: white perch were 85-205 mm and yellow perch were 85-139 mm. Although maximum food consumption rates are greater for smaller fish of a species, I made the consumption comparisons to the small yellow perch for several reasons. Generally, the white perch collected fell into the smaller size category, however, it was necessary to include the larger-sized fish because of constraints of sample sizes. The inclusion of larger fish in the calculations would
presumably decrease the consumption rate of white perch. Comparing these rates to those of the small yellow perch would therefore, result in the most conservative estimate of consumption rate differences between the two species.

The high daily ration determined for white perch in this study are even more impressive when compared to those of yellow perch in other systems and also, other species. Nakashima and Leggett (1978) estimated yellow perch (83-150 mm) daily ration in Lake Memphremagog, Quebec-Vermont to range from 2.2% in October to 6.7% in July. These results are comparable to those of yellow perch in Lake Erie. Where other species are concerned, Cochran and Adelman (1982) found that daily ration for age-3 largemouth bass ranged from almost zero in May to over 5% in August. In another study, consumption by 3-year-old walleyes averaged 1% in June and peaked at 3% in August and September (Swenson and Smith 1973).

While Lake Erie white perch consume mostly invertebrates, as they do in other systems, there are some significant differences in diets from other studies. Bath and O'Connor (1985) concluded that white perch in the Hudson River preyed primarily on benthic epifauna and infauna when they found mostly crustaceans, insect larvae and annelid worms in the stomachs. In Nebraska reservoirs, white perch ate bentho almost exclusively over zooplankton. Dipteran larvae, especially Chironomids and Ephemeropterans, were
important diet items. Fish were rarely eaten in Nebraska, although Elrod et al. (1981) found age-2 white perch were piscivorous. Previous literature reviews of white perch indicate they are extremely opportunistic in that diets are broad, and very plastic (Zuerlein 1981; Stanley and Danie 1983).

In Lake Erie, I found that although white perch ate significant amounts of benthic organisms, zooplankton were eaten by all sizes (85-205 mm) when zooplankton were abundant. When the larger zooplankton were not available, white perch ate smaller organisms such as, copepods and Eubosmina. White perch appear to be an efficient species in their ability to adapt to available prey and yet, maintain high consumption rates.

My results differ somewhat from the previous Lake Erie white perch diet information published by Schaeffer and Margraf (1986a); in September 1981, 77% of the white perch diet was gizzard shad. (Also, Knight and Margraf (1984) show inshore yellow perch being piscivorous at this same time.) In light of the results of my study, 1981 may have been an anomaly in that gizzard shad comprised such a large proportion of the diet. However, although I show results from some shallow water collecting stations in the western basin, I did not sample in Sandusky Bay, as did Schaeffer and Margraf (1986a).
High diet overlaps between white perch and yellow perch should not be a surprising result. The two species are morphologically similar, even though they are not in the same family. They are both sight-feeders with corresponding diurnal feeding patterns, which would indicate that prey availability would aptly be similar. Also, Hayward and Margraf (1987) indicate there has been a reduction in the number of species available for consumption resulting from the effects of eutrophication in the lake. A prey base with fewer species to select from should result in higher overlaps in diets for fish species of similar trophic requirements. However, exploitative competition may not be a factor if the remaining or replacement eutrophication-tolerant organisms occur in large enough numbers that consumption and ultimately, growth are not reduced.

Therefore, the most informative diet overlap results are those with divergent diets. The lowest overlap values occurred in the spring and autumn. In the spring and occasionally in the summer, yellow perch ate almost exclusively, Chironomids; white perch also preyed upon Chironomids heavily, but when a divergence occurred, white perch were usually feeding more on zooplankton. In some of the summer and autumn samples, yellow perch ate fish to a greater degree than white perch. In all of the diet overlap values calculated (n=68) and where the index was
insignificant (<0.6), white perch ate more fish than yellow perch in only one instance.

The diet overlap values become more relevant when discussed in relation to consumption rates. A paradoxical situation occurs with white perch feeding on zooplankton and yet, maintaining high consumption rates. At the same time, yellow perch are feeding on the larger-bodied benthic organisms or fish, but their consumption rates are often at or below maintenance level (Hayward and Margraf 1987). A possible explanation may be that white perch are simply efficient zooplanktivores, even as adults. They are not as subjected to ontogenetic shifts in diet that are imperative to yellow perch. Although similar morphologically, the white perch has a more terminal mouth, which is advantageous in feeding up in the water column. Yellow perch have a somewhat more subterminal mouth, making it easier to feed at the bottom.

Diet overlap results from this study indicate some differences from what Schaeffer and Margraf (1986a) found. They reported insignificant values for August and September 1981, mainly because of white perch feeding heavily on gizzard shad. As stated previously, I consider this to be an anomalous situation. The fish used for the comparisons were from non-overlapping sampling sites and times. Although the fish were collected only 5-km apart, the
possibility of differing prey availability between the two sites is likely.

In Lake Ontario, Elrod et al. (1981) found white perch and yellow perch eating similar prey. They concluded that the high overlap in diets was because of availability of organisms. Amphipods, one of the most abundant benthic organisms, were consumed heavily by both species. Because of the sparsity of benthic organisms in Lake Erie, some partitioning of that limited-resource appears to occur. If yellow perch is more dependent on being benthivorous than white perch, then it would be logical to assume that white perch feed more on zooplankton than yellow perch. This argument would be valid except in cases where benthic organisms are abundant (e.g., Chironomid emergent events) or extremely low zooplankton numbers.

Although I was unable to accurately determine individual growth of white perch in Lake Erie, I was able to discern certain characteristics of those individuals. I was unable to detect a decline in adult white perch growth from back-calculations or distinct differences in interbasin growth. If the central basin white perch are growing faster than those in the western basin, it is definitely not comparable to the interbasin growth difference shown by yellow perch.

Hayward and Margraf (1987) have clearly attributed yellow perch growth disparities to reduced food consumption
in those fish occupying the more eutrophic western basin. Interestingly, white perch show the same disparate pattern of food consumption as yellow perch, but not the same growth pattern. Possible explanations for this phenomenon could lie in physiological requirements of the two species. The thermal optimum for yellow perch is reported to be 23 C (Schneider 1973), with a maximum observed preference of 29 C in the laboratory and 27 C in the field (Hokanson 1977). The white perch optimum is at least a few degrees higher. Several thermal optima have been reported for white perch from 5 C to 32 C, which are totally dependent on the acclimation temperature (Stanley and Danie 1983). Kellogg and Gift (1983) determined that the optimum growth temperature for young white perch (approximately 30mm, TL) was 28.5 C.

These differences in thermal preferences between the two species may alter their separate abilities in using the food resource. Although differences in thermal regimes in the central and western basins of the lake are not responsible for the large interbasin growth differences of yellow perch, the white perch may have an alternate scenario. From the apparent higher thermal preference, white perch may be able to eat less in the western basin and still maintain similar growth to those in the central basin because of reduced energetic costs.
Another scenario is related to interbasin mixing of populations. Movements of white perch are essentially unknown. Although white perch are not noted for swimming long distances within their natural range of the east coast estuaries, it is quite possible that the populations of the central and western basins congregate at various times. Most likely this occurrence would be in the rivers of the western basin in spring during spawning. Because of these non-discrete interbasin populations, differences in growth would be very difficult to detect.

Although direct evidence for competition can only be determined through experimentation, I have shown that the potential for white perch to negatively affect yellow perch in Lake Erie is great. While I agree with Hayward and Margraf (1987) that the eutrophication of Lake Erie is a mechanism that is responsible for the beginnings of the disparate interbasin growth in yellow perch, the disparity has increased since the arrival of white perch. As Hanson and Leggett (1982) found in their study, fish biomass was strongly correlated to macrobenthos biomass. Given the existence of a limited food-resource, in especially the western basin of Lake Erie, yellow perch would have to be directly affected by the invasion of a new species, such as white perch, which feeds on similar prey.
Chapter 2
A Gastric Evacuation Rate for White Perch
Determined from Laboratory and Field-Collected Data

Introduction

In recent years, many fisheries studies have attempted to estimate food consumption for a variety of species (e.g., Swenson and Smith 1973; Cochran and Adelman 1983; Hayward and Margraf 1987). As a part of my study to evaluate white perch-yellow perch interactions in Lake Erie, I wished to make comparisons of white perch and yellow perch daily rations. However, in order to calculate white perch rations, I first had to determine their gastric evacuation rate as one was not available in the literature.

Full-scale laboratory evacuation rate determinations are arduous and often susceptible to erroneous results from the unnatural conditions associated with confined fish (Sainsbury 1986). However, within-sample variabilities in stomach contents from field-collected fish could also provide suspect evacuation results, since differing meal volumes used in experimentation appear to alter rates
(Jobling 1986). Although, some researchers do not agree with Jobling's conclusion (Persson 1979).

Therefore, in this study I adopted a pragmatic two-tiered approach. I combined laboratory and field-collected data for white perch to determine a single evacuation rate for use in the Elliot and Persson (1978) consumption model.
Methods

White perch (mostly age-1+, approximately 150-175 mm TL) used in the laboratory experiments were collected in Sandusky Bay during August and September 1985 by seine and otter trawl. The fish were transported to the Aquatic Ecology Laboratory (OSU) in Columbus, Ohio where the experiments were conducted.

Fish were acclimated to the ambient laboratory water (15-18 C). They were fed fathead minnows (Pimephales promelas) ad libitum for several weeks. During this time, the fish were individually marked with color coded ceramic beads that were inserted ventral to the base of the soft dorsal fin. It was necessary to individually tag the fish, because they would only feed well if kept in schools of at least six fish.

The experimental temperatures were 15 and 23 C. These were chosen because they span the majority of Lake Erie temperatures during the sampling season. Fish were acclimated to each temperature for at least 24 hours before initiation of the experiment and were starved for a period up to 4 days to allow for gut clearance and active feeding at the time of the experiment.

On the day of an experimental trial, several fathead minnows were individually weighed and then introduced sequentially into the tank containing several white perch.
The time each minnow was eaten was recorded along with the color code of the consumer. In cases of multiple prey captures, those fish were excluded from the analyses. At the end of the specified period of time for each fish, they were anesthetized with quinaldine and their stomachs evacuated using a gastric lavage technique. The recovered prey item was blotted dry and weighed. The periods of time used at 15 C was 2, 4, 6, 8, 10, and 12 hours; at 23 C, it was 1, 2, 4, 6, 8, and 10 hours. The decline in stomach contents during these experiments were expressed as the percent difference from the initial weight of the prey consumed.

Field-collected data used in this determination, were from white perch collected during diel sampling in 1983-84 and 1987 (see Chapter 1 for details of fish collection and laboratory processing). Medians of weight-specific food quantities (g/g) of fish collected during the descending phase (i.e., the nighttime, non-feeding hours) of the 24-h period were expressed in a manner similar to the laboratory experimental data. Only diel data that showed a clearly exponential decline in stomach contents during the nighttime and where temperatures ranged from 12.6 to 22 C were used.
Results and Discussion

Means and 95% confidence intervals of percent food remaining in stomachs of fish in the laboratory experiments at 15 C (Fig.36) and 23 C (Fig.37) are shown. Each point estimate represents between four and seven stomachs. The 23 C experiments were run only to 10 hours, because of problems associated with empty stomachs appearing in the analysis (Olson and Mullen 1986). Both curves follow the exponential function of gastric evacuation as described by Elliot (1972). R, the instantaneous rate of gastric evacuation, which is the slope of the log-transformed regressions, is given for each temperature from the laboratory experiments and the field-collected data (Table 7).

Elliot (1972) also defined the relationship of R and temperature by an exponential function: $R=ae^{bT}$, where a and b are constants and T is the temperature. For white perch, I determined that this relationship was $R=0.028e^{0.106T}$ ($r^2=0.98$). Persson's R (1979) for European perch (Perca fluviatilis) was $R=0.018e^{0.14T}$. Hayward and Margraf (1987) used Persson's R for European perch in the calculation of yellow perch consumption in Lake Erie. These relationships for white perch and yellow perch (=European perch) are shown (Fig.38), along with those for brown trout (Salmo trutta) (Elliot 1972) and largemouth bass (Micropterus salmoides) (Cochran and Adelman 1982).
Figure 36. Means and 95% confidence intervals of percent food remaining from 0-12 hours after ingestion at 15 (C) as determined in laboratory evacuation experiments.
Figure 37. Means and 95% confidence intervals of percent food remaining from 0-10 hours after ingestion at 23 (C) as determined in laboratory evacuation experiments.
Table 7. The slopes and \( r^2 \) values for the log-transformed data from laboratory experiments (15 and 23 C) and diel field-collections (12.6, 16, and 22 C).

<table>
<thead>
<tr>
<th>Temperature (C)</th>
<th>Slope (b)</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.6</td>
<td>-0.095</td>
<td>0.80</td>
</tr>
<tr>
<td>15.0</td>
<td>-0.148</td>
<td>0.99</td>
</tr>
<tr>
<td>16.0</td>
<td>-0.160</td>
<td>0.95</td>
</tr>
<tr>
<td>22.0</td>
<td>-0.280</td>
<td>1.0(^a)</td>
</tr>
<tr>
<td>23.0</td>
<td>-0.313</td>
<td>0.95</td>
</tr>
</tbody>
</table>

\(^a\)Only two data points available.
Durbin et al. (1983) summarized much of the current literature available on gastric evacuation rates concerning several marine and freshwater fishes. They concluded the following:

1) Most experimental gastric evacuation data can be described by an exponential model. The model provides good estimates of food consumption using the formulation of Elliot and Persson (1972).

2) Temperature and food type are the two factors that strongly influence $R$, but multiple meals do not.

3) Although the intercepts ($a$) of the evacuation rate and temperature relationships varied according to different prey types, the slopes ($b$) were similar for several marine and freshwater fishes.

Other recent literature argues concerning the choice of an appropriate evacuation model. Mullen (1986) and Olson and Mullen (1986) indicate that some relationships are linear and therefore, the use of the exponential model is not valid. Persson (1986) points out advantages to using the exponential model over the square root model, which does not have physiological rationale. Jobling's (1986) results predicted that the exponential model best fits those species consuming smaller, easily digested items, while the linear model is a better fit for fish consuming large-sized prey.
Although type of food has been reported to affect gastric evacuation rates, either directly or in altering the fit of a single model, Persson (1979) reported conflicting results from studies using variable prey sizes. The approach I adopted in this study was to use large, single prey items that could be accurately weighed in various stages of digestion. When these data were plotted, the relationship was clearly exponential. Therefore, I used only diel information that showed an exponential decline in food present in the stomachs during the non-feeding hours to represent the same relationship. The resulting high $r^2$ (0.98) is testament to the good fit of the data.

Persson (1986) and Jobling (1986) describe the physiological basis of digestion and the role of temperature in that process. Therefore, temperature ranges used in determining gastric evacuation rates are critical. For brown trout, Elliot (1972) used temperatures ranging from 5.2 to 15 C. Persson (1979) used a range of 4.0 to 21.7 C in his experiments with the European perch. These ranges are reflective of temperatures occupied by both species in their natural habitats. Thus, I chose the range of 12.6 to 23 C as representative of white perch in Lake Erie. Although white perch are exposed to other temperatures in the lake, this range is reflective of the temperatures during the period of sampling.
In Fig. 38, I show the evacuation relationships of white perch, yellow perch, brown trout, and largemouth bass. I chose these other species from the literature to illustrate the ranges of values from coldwater to warmwater species. The fact that my white perch relationship is most similar to that of yellow perch and that these two mesotherms lie between the coldwater and warmwater species, gives credence to this relationship as determined.
Figure 38. The relationship between instantaneous gastric evacuation rate (R) and temperature in white perch and three other freshwater fishes: Brown trout (Elliot 1972), yellow perch (Persson 1979), and largemouth bass (Cochran and Adelman 1982).
Chapter 3
Feeding Selectivities of YOY White Perch and
Yellow Perch in Laboratory Experiments

Introduction

In Lake Erie, YOY fishes of many species, including white perch and yellow perch, feed almost exclusively on zooplankton. Given that white perch and yellow perch interact throughout their ontogeny, I investigated various aspects of their feeding on zooplankton prey. In the laboratory, I conducted experiments using YOY white perch and yellow perch. These feeding selectivity experiments involved introducing a "natural mix" of Lake Erie organisms, collected in plankton samples, into tanks where both fish were held in allopatry and sympatry.

In conducting these experiments I asked the following question: Given a known quantity and species distribution of zooplankton prey, do white perch and yellow perch consume the same prey in allopatry and sympathy? Knowing the feeding preferences of these two species aids in predicting how white perch and yellow perch partition their available resource.
Methods

YOY white perch and yellow perch were collected by shoreline seining and some bottom trawling in Lake Erie. The fish were transported to the OSU F.T. Stone Laboratory at Put-in-Bay, Ohio where the experiments were conducted.

In August 1986, I ran three trials of this experiment in which YOY white perch and yellow perch feeding selectivities were examined when held in laboratory aquaria in allopatry and sympatry. I stocked both species into a three-partitioned 200-L stream tank as follow:

<table>
<thead>
<tr>
<th># of Trials</th>
<th>White Perch : Yellow Perch</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>10:0, 5:5, 0:10</td>
</tr>
</tbody>
</table>

White perch and yellow perch were held in the laboratory a minimum of 4 days and were acclimated for at least 24-h to the tank before the experiment. Fish were starved for 18-24h to allow for gut clearance. The zooplankton sample was collected at dawn with a 118-um mesh net using vertical plankton tows. At approximately 0700h, three 116-ml aliquots were introduced into the partitioned tank. A fourth aliquot was preserved in 10% formalin for determining zooplankton abundance and species composition. Triplicate subsamples were counted and averaged. The averages of this aliquot represents the available organisms for consumption in the "environmental" samples.
Seven minutes after the prey were introduced, I froze all fish for later analysis. At the time of work-up, fish were thawed, standard lengths (mm) recorded, and stomach contents identified and counted. I compared the proportions of prey consumed by the two species with the proportion available in the environment to calculate the selectivities (Manly/Chesson index; Chesson 1978, 1983).

In September and October 1987, five additional trials of this experiment were run. However, there were some changes in the procedure that should be noted. Fish were stocked in three separate 750-L aquaria. Prior to collection of the plankton sample, each tank was drained to a level of approximately 100-L, so the plankton would be concentrated. Samples were collected just before dawn towing horizontally with a 505-μm plankton net. Fish were allowed to eat for 10 minutes, with timing beginning when the first fish initiated feeding. All of the other parts of the procedure were essentially the same as that used in 1986.
Results

The "environmental" samples species compositions differed from 1986 to 1987 and within years according to numbers of organisms available (Table 8). Although Ostracods are usually not considered a part of the plankton, they were collected in two trials in 1986 and were consumed by the fish. Only cyclopoid copepods were present in 1986, but both cyclopoid and calanoid copepods were present in 1987. *Bythotrephes*, the newly invading European cladoceran, was not present in 1986; in 1987, it was present in only the latter two trials. *Diaphanosoma* and some chydorids were present only in sparse numbers in one trial, so they were not considered in the selectivity calculations.

There were few differences in mean numbers of organisms eaten by white perch and yellow perch in allopatry and sympatry in 1986 (Table 9). Manly/Chesson preference index values, with values indicating positive selection underlined, show many similarities between species (Table 10). Although very few differences are evident, yellow perch selected for *Leptodora* and white perch did not. However, white perch selected for Ostracods. Both species selected *Daphnia* and cyclopoid copepods. These patterns were regardless of the allopatric or sympatric condition.

The 1987 results (Tables 11 and 12), are somewhat different from those of 1986, although being in allopatry or
Table 8. Numbers of organisms from plankton samples introduced into each compartment or tank during YOY feeding selectivity experiments in 1986 and 1987. LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, CAL=calanoid copepods, EUB=Eubosmina, OST=Ostracods, and BYT=Bythrotrephes.

<table>
<thead>
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<th>Trial</th>
<th>Date</th>
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<th>CYC</th>
<th>EUB</th>
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<td>2</td>
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<tr>
<td>3</td>
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<td>70</td>
<td>310</td>
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<td>48</td>
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1987

<table>
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Table 9. Mean numbers of organisms eaten during white perch (WP) and yellow perch (YP) allopatric-sympatric feeding selectivity experiments in 1986. LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, EUB=Eubosmina, and OST=Ostracods. N=number of fish.

<table>
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<th>TRIAL</th>
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<th>DAP</th>
<th>CYC</th>
<th>EUB</th>
<th>OST</th>
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</thead>
<tbody>
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<td>7.2</td>
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<td>b</td>
</tr>
<tr>
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<td>7.2</td>
<td>73.0</td>
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\(^a\)A = Allopatric; \(S = \) Sympatric.

\(^b\)Ostracods were not present in the plankton samples.
Table 10. Preference values (Manly/Chesson index) for white perch (WP) and yellow perch (YP) from allopatric-sympatric feeding selectivity experiments in 1986. LEP=Leptodora, DAP=Daphnia, CYC=cyclopod copepods, EUB=Eubosmina, and OST=Ostracods. Preferences > .25 in trial 1 and > .20 in trials 2 and 3 are underlined, indicating positive selection for a given prey. N=number of fish.

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\[^aA = Allopatric; S = Sympatric.\]

\[^bOstracods were not present in the plankton samples.\]
Table 11. Mean number of prey eaten by white perch (WP) and yellow perch (YP) from allopatric-sympatric feeding selectivity experiments in 1987. LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, CAL=calanoid copepods, EUB=Eubosmina, and BYT=Bythrotrephes. N=number of fish.

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<sup>a</sup>A = Allopatric; S = Sympatric.

<sup>b</sup>Organism was not present in the plankton sample.
Table 12. Preference values (Manly/Chesson index) for white perch (WP) and yellow perch (YP) from allopatric-sympatric feeding selectivity experiments in 1987. LEP=Leptodora, DAP=Daphnia, CYC=cyclopoid copepods, CAL=calanoid copepods, EUB=Eubosmina, and BYT=Bythotrephes. Preferences > .20 in trials 1-3 and 5 and > .17 in trial 4 are underlined; indicating positive selection for a given prey. N=number of fish.

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*a* A = Allopatric; S = Sympatric.

*b* Organism was not present in the plankton sample.
sympathy was still not a factor. Yellow perch never selected for *Leptodora*, but white perch did in one trial. Neither species selected *Daphnia*, but both did eat the copepods and to a lesser degree, *Eubosmina*. Sympatric yellow perch selected for *Bythrotrephes* in one trial.

The data from the three trials in 1986 were pooled for use in the ANOVA and MANOVA analyses (Table 13). The 1987 data could not be handled similarly because of entire tanks of fish not eating during some of the trials (Table 14). From the ANOVAs, which tested for differences of individual prey items, only differences in *Leptodora* were present in 1986. In the 1987 ANOVAs, the significant differences were in *Leptodora* and *Eubosmina*. In some of the 1987 trials, few fish were feeding and results of significance should be interpreted with caution. I ran MANOVA procedures to test for differences in the entire feeding array between species and within species in allopatry and sympathy. None of the MANOVA results were significant.
Table 13. ANOVA and MANOVA results (Allopatric vs. Sympatric within a species; Between the two species) of preference values (Manley/Chesson index) of prey consumed by white perch and yellow perch during the three trials of the 1986 YOY feeding selectivity experiments. NS=Not significant (P > 0.05).

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<td>Eubosmina</td>
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<td>Ostracods</td>
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<td>MANOVA--1986</td>
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Table 14. ANOVA and MANOVA results (Allopatric vs. Sympatric within a species; Between the two species) of preference values (Manley/Chesson index) of prey consumed by white perch and yellow perch during 1987 YOY feeding selectivity experiments. Results are presented by trials. NS=Not significant (P > 0.05), NA=Not available.

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Discussion

The results of these selectivity experiments indicate that white perch and yellow perch are equally capable of feeding on zooplankton. There were essentially no differences in allopatry and sympatry within a species or between species, which shows a lack of interspecific competition among YOY white perch and yellow perch. This laboratory situation can be extrapolated to the field given that resources are not limiting. Although prey depletion was possible in the experiments, which presents problems in respect to calculating preferences (Chesson 1983), usually many organisms were not eaten. Only Leptodora may have fallen into this category in 1986 (Table 7). So, although I now know that both species are similarly capable of feeding on available zooplankton in Lake Erie, I can not yet make conclusions concerning their abilities in extremely low zooplankton concentrations.

After finding only the Leptodora difference in the 1986 experiments, I altered some parts of the procedure in 1987. I altered the plankton net towing time, so that different concentrations of organisms were introduced; only the fifth trial had very few organisms in some of the tanks, but few fish were feeding. I used a larger mesh plankton net in 1987 and did horizontal tows in an effort to collect more of the larger species such as Leptodora and Bythotrephes. Also
in 1987, the experiments were run in September and October, while in 1986 they were in August. This not only altered the prey composition, but also the fish were of different sizes. Fish in 1986 ranged from approximately 44-55 mm and in 1987 ranged from 55-80 mm. None of these alterations had an overwhelming effect on the experiment outcome.

Following the competition aspect of this experiment, I was most interested in examining what organisms both species ate. Much has been written concerning which prey a fish "should" consume, according to the size-efficiency hypothesis (Brooks and Dodson 1965), to optimize its energy intake and increase its fitness (optimal foraging theory: Charnov 1976). Werner and Hall (1974) found that prey were eaten as encountered at low densities, while size-selectivity operated when densities were high. Also, animals should be more selective when satiated (Emlen 1966).

In these experiments, I found that white perch were generally not eating the largest prey (Leptodora in both years and also, Bythotrephes in 1987). However, yellow perch did in 1986. They both selected the most numerous prey as a rule in 1986, but in 1987 consumed cyclopoid and calanoid copepods more than the most numerous prey, Leptodora and Daphnia. These results are somewhat puzzling, but could possibly be related to an overall lack of intensive feeding during some of the experimental trials.
Other researchers have investigated prey selection of young yellow perch. Hansen and Wahl (1981) found that yellow perch from field collections ate the smaller prey of those sizes available, even though the fish were capable of ingesting the larger ones. Their hypothesis was that young fish are less successful in capturing large prey. Mills et al. (1984) conducted laboratory feeding experiments with young yellow perch and zooplankton prey, in which they also found the fish eating smaller organisms. However, their data showed that yellow perch were capable of capturing the largest daphnids and should elect to consume those items. They concluded that yellow perch may digest larger daphnids inefficiently, resulting in consumption of the smaller ones.

From these studies (Mills et al. 1986) and others (Furnass 1979; Mittelbach 1981), it is evident that young planktivorous fish feed in patterns inconsistent with optimal foraging theory. Speculation is that reduced searching ability, handling efficiency, and ability to detect size differences in prey may affect prey selection by young fish (Mittelbach 1981). Therefore, the deviations from expected selectivities in my experiments may be related to these same inabilities. Based on my results and those of previous workers, more experiments need to be conducted to capably predict optimal foraging in young fish.
Chapter 4
YOY White Perch and Yellow Perch in situ
Field-Enclosure Experiments

Introduction

As noted in Hanson and Leggett (1985), three methods have been used to study competitive interactions in fish communities. The first is niche overlap, which assumes that some resource is limiting (e.g., see Chapter 1). The second method involves niche shifts, where patterns of resource usage are examined under allopatric and sympatric conditions. Although these are generally field studies called "natural experiments", laboratory feeding selectivity experiments can also be in this category (see Chapter 2).

However, the current best method for detecting competition in fish communities is the controlled field experiment, usually using enclosures in a natural setting. Hanson and Leggett (1985) have conducted competition experiments with yellow perch and pumpkinseeds (Lepomis gibbosus), and Mittelbach (1988) did a similar study using bluegills (Lepomis macrochirus) and pumpkinseeds. In this chapter, I present results from in situ field-enclosure experiments that I performed at Lake Erie in 1986 and 1987 using YOY white perch and yellow perch.
Methods

The experiments were conducted in Lake Erie near OSU's Gibraltar Island. In 1986, YOY white perch and yellow perch were collected by shoreline seining around South Bass Island and bottom trawling from the OSU Biolab near East Harbor. Trawling consisted of making 2-3 minute tows at a depth of 3-5 m. White perch and yellow perch from the trawls were placed in an aerated 238-l tank for the 1-h transport to OSU's Stone Laboratory. The water temperature was held constant by adding ice as necessary.

Fish were held in laboratory Lake Erie running-water aquaria a minimum of 48-h before stocking in the cages. Zooplankton collections were added to the tanks to supplement the fish diets during this time.

The experimental design of numbers of fish stocked in each cage are given for the two trials in 1986 and the one in 1987 (Table 15). Each fish was weighed to the nearest 0.01 g and measured (SL, mm). Fish were anesthetized with quinaldine prior to handling, but were allowed to fully recover before stocking.

The experiments in 1986 were performed in 6 (1.2 x 1.2 x 1.2 m) wooden cages with 3-mm wire mesh. The cages were arrayed linearly along the south Gibraltar Island shoreline approximately 10-m from shore in 2.6-m of water. The cages floated at the water surface and were held in place tethered
Table 15. Numbers of white perch (WP) and yellow perch (YP) placed at random into each cage (6 in 1986 and 12 in 1987).

<table>
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to anchors. The first trial in 1986 ran from August 8 to August 20 (12 days) and trial 2 was from August 22 to September 7 (15 days). Mean standard lengths of yellow perch stocked in trial 1 were 48.0 mm and those of white perch were 42.8 mm. In trial 2, they were: yellow perch at 52.4 mm and white perch at 50.6 mm.

In 1987, the type and number of cages were changed. Twelve cylinder-shaped (1.1 x 1.2 m) cages were constructed of 4-mm mesh plastic netting attached to fiberglass hoops. Floats were attached to the tops to keep the cages at the surface. The cages were tethered to trapnet anchors and arranged along the shoreline as was done in 1986.

In 1987, because of a yellow perch year-class failure in Lake Erie, I collected yellow perch in Lake Huron. The fish were seined during the early morning until late afternoon (September 28) from Saginaw Bay at Pinconning State Park north of Bay City, Michigan. The fish were held in an aerated transport tank until 0830 h on September 29. The water temperature remained constant at 18 C, which was also the Lake Erie water temperature. The tank was checked every two hours during the night and approximately one-fourth of the water was exchanged twice. Of 211 yellow perch, only two died in transport.

Yellow perch were held in the laboratory for 15 days and fed zooplankton daily. The white perch were all collected on October 13 at Perry's Monument beach. The
experiment then began on October 15 and ran until November 6 (22 days). Mean standard lengths of yellow perch were 70.9 mm and those of white perch were 72.6 mm. The lake water temperature declined from 11.1 to 7.3 °C during the experiment.

During both years, integrity of the cages and fish mortalities were checked daily. At the end of each trial, fish were removed from the cages, bagged (by cage), and kept on ice until weighed and measured.
Results and Discussion

In these experiments, I asked the following questions. Do white perch numbers affect yellow perch growth? Do numbers of fish, either white perch or yellow perch, affect white perch growth? My approach to these experiments was very similar to that of other fish competition work using field experiments (Hanson and Leggett 1985; Mittelbach 1988).

In trial 1 of 1986, both yellow perch and white perch growth declined linearly according to total fish in each cage (Figs. 39 and 40). The regression lines are: $Y = 0.55 - 0.016X$, $r^2 = 0.73$ for yellow perch and $Y = 1.38 - 0.05X$, $r^2 = 0.58$ for white perch. Although both species have negative regression slopes, the null hypothesis of a slope of 0 is not rejected at $P < 0.01$. Mortality was quite high in trial 1, especially for white perch, and may have affected the results. The occurrence of a major storm event a few days post-stocking was a likely factor in the loss of fish.

The results of trial 2 in 1986 (Figs. 41 and 42) can be explained in two ways. First, the total numbers of fish in the cages at the end of the experiment ranged from 14-19. This restricted range would not permit large enough differences in growth to be detectable. The other problem in this trial concerns the assumption of food-limitation.
Figure 39. Mean growth of yellow perch as a function of white perch and yellow perch densities during trial 1 of 1986 cage experiments.
Figure 40. Mean growth of white perch as a function of white perch and yellow perch densities during trial 1 of 1986 cage experiments.
Figure 41. Mean growth of yellow perch as a function of white perch and yellow perch densities during trial 2 of 1986 cage experiments.
Figure 42. Mean growth of white perch as a function of white perch and yellow perch densities during trial 2 of 1986 cage experiments.
During the time the cages were in the water, amphipods colonized the cages. I did not see the amphipods on the cages at the end of trial 1, and the fish stomachs contained only a few. However, upon examination of the fish stomachs from trial 2, amphipods had been consumed by most of the fish.

When comparing white perch growth with that of yellow perch in 1986, white perch clearly showed better growth during trial 1 than did yellow perch (Fig. 43). In trial 2, five of the points indicated that both were growing equally well.

The 1987 results also were not anticipated (Figs. 44 and 45). However, a somewhat clearer relationship is shown when examining both yellow perch and white perch growth as a function of their total numbers per cage (Fig. 46). This regression line is $Y = 0.72 - 0.018X$, $r^2 = 0.52$ and a regression slope of 0 is rejected at $P < 0.01$.

The 1987 trial had several confounding effects that could help explain the results. Because of the poor year-class of yellow perch in Lake Erie, I resorted to using Lake Huron yellow perch. I arrived at this decision too late in the growing season to obtain optimal growth of the fish during a short-term experiment. Water temperatures declined rapidly, so feeding for both species was much reduced from those levels during August and early September.
Figure 43. White perch vs. yellow perch mean growths (with 45° line drawn) from trials 1 and 2 cage experiments in 1986.
Figure 44. Mean growth of yellow perch as a function of white perch and yellow perch densities during 1987 cage experiment.
Figure 45. Mean growth of white perch as a function of white perch and yellow perch densities during 1987 cage experiment.
Figure 46. Mean growth of total fish (white perch and yellow perch) as a function of total fish densities during 1987 cage experiment.
However, this experiment proved to be interesting from an energetic viewpoint. Yellow perch grew during this time, regardless of white perch densities (Fig. 44), while most of the white perch declined in weight (Fig. 45). When combined and as a function of total fish in a cage, white perch and yellow perch growth showed a negative relationship according to increased fish density (Fig. 46). So, yellow perch were feeding and maintaining their weight, while white perch were either not feeding or feeding minimally. Therefore, white perch densities did not alter yellow perch growth.

It is known that yellow perch feed throughout the winter (Keast 1968), but the extent of white perch feeding at low temperatures is not known. From my laboratory work in 1985, I know that white perch feed at 5°C, but only at or just below maintenance level. Also during this experiment, the differences in thermal optima (see Chapter 1) between the species could be a factor in yellow perch continuing to feed at a higher level later in the season.

Unfortunately, my results do not provide unequivocal evidence for interspecific competition between YOY white perch and yellow perch in Lake Erie. These results, however uncompelling, do indicate that the potential for competition between these species does exist and further investigations should be able to elucidate that interaction.
SUMMARY

Following the white perch invasion into Lake Erie, yellow perch individual growth rates declined to an even greater degree than previously noted. Because white perch and yellow perch have been consistently collected together in Lake Erie, I investigated their potential interaction by determining and comparing consumption rates, diets, and individual growth from field-collected data in 1983-85 and 1987.

From these data, I was able to draw several conclusions. White perch exhibited interbasin consumption rate differences similar to those of yellow perch (i.e., white perch ate more in the central basin than in the western). White perch usually ate more than yellow perch when compared by basin, and white perch daily rations in the central basin of Lake Erie exceeded those of most species reported in the literature.

White perch generally fed more on zooplankton or smaller benthic organisms in Lake Erie than they do in many other systems where the benthos is more productive. Diet overlaps of white perch and yellow perch were especially significant (Schoener index > 0.6) during the summer months.
During the three year period, of 68 overlap comparisons, 52% were significant. The lowest index values were in the spring and fall when yellow perch were more benthi- vorous or piscivorous, while white perch consumed more zooplankton.

Although white perch showed interbasin differences in consumption, these differences did not result in a large growth disparity as that occurring in yellow perch (i.e., yellow perch in the western basin grow much slower than those in the central basin). I have surmised that this phenomena could result from a higher thermal preference or movements of white perch that do not allow for discrete populations. In either case, the western basin of Lake Erie could present a more optimal environment and therefore, consumption might be lower than in the central basin and still result in similar growth.

As a part of this study, I had to determine a gastric evacuation rate for white perch in order to use the Elliot and Persson (1978) consumption model. I conducted laboratory experiments and used diel field-collected data in making this determination. The resulting relationship of $R$ and temperature for white perch was $R=0.028e^{0.106T}$. This rate compares well with those available for other species, and especially for yellow perch.

Also, I performed zooplankton feeding selectivity experiments with YOY white perch and yellow perch in allopatry and sympatry. These experiments were performed to
assess the feeding capabilities of YOY of both species and to determine if feeding patterns were altered in the sympatric condition resulting from either interference or exploitative competition. From the results of these experiments, I concluded that both species are equally capable of feeding on zooplankton and both showed no differences whether in allopatriy or sympatriy. Although there were a few differences between the two in use of individual prey categories (ANOVA results), feeding on the entire array of organisms available was not different (MANOVA results). Although, prey selection by white perch and yellow perch did not follow optimal foraging theory, my results agree with other previously published research using young fish.

In the final part of this study, I conducted in situ field-enclosure competition experiments with YOY white perch and yellow perch. The main purpose of these experiments was to determine if white perch numbers affected yellow perch growth and if fish density, regardless of species, affected white perch growth. My results did not provide unequivocal evidence for interspecific competition, although in two of the three trials, there was a negative relationship of fish growth as a function of fish numbers. Also, white perch growth was not as affected by increased fish densities as was yellow perch.
LIST OF REFERENCES


Hayward, R.S. 1988. Eutrophication effects on biocenetic conditions for Lake Erie yellow perch. Doctoral dissertation. The Ohio State University, Columbus, Ohio.


Schaeffer, J.S. 1984. The white perch of Lake Erie; the ecology of an invading species. M.S. Thesis, The Ohio State University, Columbus, Ohio, USA.


