The effects of life history parameters on the reproductive potential of yellow perch (\textit{Perca flavescens}) populations

by

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A thesis submitted in conformity with the requirements for the degree of Master of Science Graduate Department of Zoology University of Toronto

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The effects of life history parameters on the reproductive potential of yellow perch (*Perca flavescens*) populations

Master of Science, 2000
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ABSTRACT

Yellow perch populations in Lake Erie exhibit large yearly fluctuations in year class strength (YCS), with most years showing relatively poor recruitment. For percids, no statistically significant relationship between stock and recruitment has been found. Most research has focussed on various environmental factors to explain the variability in YCS. Of the studies reviewed in the first chapter, variations in YCS could not be explained by variation in any single environmental factor. The second chapter revisited the theoretical equation that spawning stock size is related to recruitment. Yearly variation in the number of mature females in the spawning stock may explain the variability in the YCS of perch. We found that the proportion of fish at age varied annually from 1978-1990, suggesting that intermittent reproduction exists for Lake Erie yellow perch. The third chapter evaluated through a model whether variation in the proportion mature as well as interannual variations in age distributions, size and the associated size-related fecundity could explain the variability in YCS of the yellow perch populations. Variation in the proportion mature could explain a large proportion of the observed YCS, however we could not accurately predict recruitment from the variations in the life history parameters included in the model.
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STRUCTURE OF THESIS

Chapter 1: A historical look at impacts to Lake Erie and the fish community. Reviews a number of studies for abiotic (temperature, wind) and biotic (predation, competition) variables and attempts to resolve the issues of the relationship between year class strength and these environmental factors.

Chapter 2: Revisiting the theoretical relationship between spawning stock size and recruitment. Factors affecting maturation are considered.

Chapter 3: Model of effect of variations of growth and maturity on population egg production.
Chapter 1:

Lake Erie ecosystem, fisheries and hypotheses
A fisheries-oriented history of Lake Erie

The Great Lakes are the largest freshwater systems in the world, holding 18% of all the world’s surface freshwater while their basins contain rich natural resources. The lakes contain 23,000 km$^3$ of water and cover a total area of 24,400 km$^2$: only the polar ice caps have more freshwater (Fuller and Shear 1995).

Despite their immense sizes, these lakes are sensitive to a wide range of anthropogenic changes (Fuller and Shear 1995). The Great Lakes are an important physical and cultural heritage of North America and these inland seas have provided water for consumption, transportation, power, recreation and livelihoods from resource exploitation. Pollution from human activities has substantially degraded the water quality in these lakes. Pollutants from urbanization, agriculture and industrialization make their way into the lakes from groundwater, rivers and streams and through direct atmospheric fallout. Of all the Great Lakes, Lake Erie has been the most affected by these anthropogenic changes.

Historical changes in Lake Erie and its effects on the fish community

Physical characteristics of Lake Erie

Lake Erie is 388 km long and 92 km wide and is the warmest and southernmost of all the Great Lakes. It has the smallest volume (475.1 km$^3$ or 2.07% of the volume of five Great Lakes) and is exposed to the greatest effects from urbanization and agriculture because of the fertile soils surrounding it. The lake is divided into three basins: western, central and eastern where the trophic status ranges from meso-eutrophic in the west to oligotrophic in the east. Although the surface area is large, the average depth ranges from 7.4 m (west
basin) to 24.4 m (east basin): overall. Lake Erie is the shallowest of all five lakes. Thus. Lake Erie warms rapidly in the spring and summer and frequently freezes in winter.

Native fish community

Lake Erie has always yielded the greatest diversity of commercially important fishes of all the Great Lakes. There have been 138 species of fish recorded in the lake at one time or another and of those, 19 species have contributed to significant harvests (Hartman 1972). The fish community in Lake Erie has included a mixture of coldwater and warmwater species. Highly-valued native fishes that dominated the fisheries from 1915 when complete fishery statistics were first available, through to the 1960's include coregonines (lake herring, longjaw cisco, lake whitefish), native salmonines (lake trout and brook trout), and percids such as sauger, blue pike and walleye (Hartman 1972: Regier and Hartman 1973). Smallmouth and largemouth bass, muskellunge, northern pike, channel catfish, freshwater drum and lake sturgeon are other native fishes that contributed significantly to the landings (Hartman 1972: Regier and Hartman 1973).

However, over the years there have been changes in the composition of exploitable fish species as a result of various human activities. Lake sturgeon, northern pike, muskellunge, channel catfish and lake herring have become rare, while native lake trout, longjaw cisco, sauger and blue pike have gone extinct (Koonce et al. 1996). The present fishery is dominated by walleye, yellow perch, white perch, white bass, lake whitefish and rainbow smelt (Koonce et al. 1996: OMNR 1997). The human activities that have generated these changes are discussed below.
Impacts
Habitat Alterations

The first serious impacts on the drainage basin and the lake resulted from harvesting timber, burning savannas and draining swamplands for agriculture, and building dams (Regier and Hartman 1973). These caused increased soil erosion leading to greater siltation rates in the rivers and nearshore areas of the lake. Spawning areas of many commercially valued species (such as walleye and the lake whitefish) were degraded due to the increased deposits of fine silt and clay burying eggs and restricting oxygen supply (Regier and Hartman 1973). In addition, once the hundreds of mill dams were built, they restricted access of fish such as sturgeon and walleye to upstream spawning habitats (Regier and Hartman 1973).

Eutrophication
Changes to conditions

Before European settlement in the 1880's, Lake Erie had mostly clear water, free of algal blooms and containing low concentrations of nutrient ions and organic substances (Fuller and Shear 1995). As the population in the drainage basin grew from 0.5 million in 1840 to 11.1 million people today, effluents increasingly made their way into the lake (Fuller and Shear 1995). By the 1960's, accelerated eutrophication through nutrient loading from agricultural practices, sewage, and detergent use had been responsible for massive algal blooms causing putrescence, floating debris, bacterial contamination and eventually extensive anoxic conditions.
Effects on benthos and fish

Anoxia resulting from eutrophication led to the decline of several organisms. The fallout of dead organic matter from greatly increased phytoplankton production had enormous effects on the bottom fauna. The low oxygen concentrations resulting from the bacterial decomposition of large deposits of organic matter led to the decline of various oxygen-sensitive benthos such as the burrowing mayfly (*Hexagenia*), an important food source for many benthivorous fishes such as yellow perch.

Catches of many coldwater fishes such as lake trout, lake herring, lake whitefish and blue pike began to fluctuate widely in the late 20's and declined to commercial extinction by the end of the 1950's (Hartman 1972; Regier and Hartman 1973; Nepsey 1977). Because these fishes require cold temperatures, they inhabit the cold hypolimnia in stratified lakes in the summer. Furthermore, they need well-aerated water of at least 5 mg dissolved oxygen/L (Davis 1975). The major effect of eutrophication may have been the gradual restriction of suitable spawning, feeding, and resting habitats for these species (Regier and Hartman 1973). From 1920-1950 there was progressive degradation of summer oxygen regimes in the bottom waters of the western and central basins (Hartman 1972). By 1953 dissolved oxygen in the bottom waters of the central basin dropped from the usual concentration of about 9 mg/L to about 1 mg/L (Regier and Hartman 1973), so these particular fish species would have experienced physiological stresses such as suffocation or having to move into warmer waters outside their optimum temperature ranges to access higher oxygen concentrations. It’s no wonder that the last major remnants of these populations were confined to the deep eastern basin (Hartman 1972).
By 1971, the hypolimnion of even the small, deep eastern basin experienced moderately low oxygen levels of 2-5 mg/L (Hurtman 1972). Although no one can deny that these populations were heavily fished, few would argue that the ultimate demise of these coldwater species was accelerated by declines in the hypolimnetic oxygen concentrations caused by eutrophication.

**Restoration efforts**

Restoring year-round aerobic conditions to the central basin became a necessary prerequisite to the reversal of fish stock losses. In 1969, a report filed by the International Joint Commission (IJC) indicated that eutrophication was the primary threat to the Lake Erie ecosystem. The concern over the degradation of water quality in Lake Erie led to the development and implementation of programs by the U.S. and Canadian governments to restore and enhance the water quality of all the Great Lakes, particularly Lake Erie (Regier and Hartman 1973: Makarewicz and Bertram 1991). The first action was to limit phosphorus inputs by improving municipal waste facilities, limiting fertilizer use and virtually eliminating phosphorus from household detergents (Makarewicz and Bertram 1991: Nicholls and Hopkins 1993). This action was no small feat. The U.S. and Canadian governments have together invested a total of 7.5 billion dollars since 1972 to improve municipal waste facilities and help industries to improve detergents and fertilizers (Makarewicz and Bertram 1991). By 1985, all municipal waste facilities on Lake Erie were in compliance with the 1.0 mg/L phosphorus limitation on effluent and annual phosphorus loadings from U.S. and Canadian municipal discharges were reduced by 84% (Makarewicz and Bertram 1991). As a result of decreased nutrient loadings, a
70%-98% reduction in many nuisance species of phytoplankton was observed (Makarewicz 1993). This action to reduce phosphorus loadings resulted in a reduction in the productivity of the lake leading to the decline in many planktivorous fish such as alewife (Alosa pseudoharengus), spottail shiner (Notropis hudsonius), and emerald shiner (Notropis atherinoides) (Makarewicz and Bertram 1991). However, eutrophication was not the only concern of fishery biologists. Toxins, exotic species and fishery exploitation were other possible causes of the changes to the lake ecosystem and fish community.

Toxins

As industrialization progressed and agriculture intensified in the late 19th and early 20th centuries, direct discharges of chemicals used in industrial processes and farming practices entered the lake largely untreated. Agricultural toxins included pesticides, herbicides and fungicides. Toxins such as DDT, dieldrin, PCBs, PCHs, benzenes. TCDD (a dioxin) are just a few of the chemicals added to the lake that are known to bioaccumulate and biomagnify in the fat of many organisms.

Toxins may have contributed to the declines of various fish species. These toxins have been found to interfere with endocrine function, reproduction and development in laboratory studies on birds, fish and mammals (MNR 1985: Leatherland 1993). An example of such effects is 2,3,7,8-TCDD, a form of dioxin that mimics estrogen, leading to the potential feminization of sex organs in males and disruption in the development of other sexual characteristics (MNR 1985: Leatherland 1993). It is also known to inhibit fat accumulation in females, a required process for the development of eggs (MNR 1985:
Leatherland 1993). In the Great Lakes, toxins have been associated with great reductions in the populations of cormorants, ospreys and herring gulls inhabiting the Great Lakes (Leatherland 1993); however, the effects of toxins on fish populations are still unclear. Toxin contamination was the reason for the complete closure of the very valuable walleye fishery in 1970. Fishing in the western and west-central basin of Lake Erie was completely banned because of unacceptable levels of mercury contamination in the flesh of the walleye species (Leach and Nepszy 1977). At the time, the effects of this stress on the fish stock itself was not fully evaluated (Leach and Nepszy 1977). Most researchers have attributed the walleye declines during 1955-75 to fishing, because when the fishing ban was put into place, walleye stocks recovered. However, the initial decline may have very well been exacerbated by mercury contamination (Regier and Hartman 1973). Recent work investigating why no self-sustaining stocked populations of various salmonids exist in Lake Ontario has prompted research into the effects of organochlorine contaminants on the mortality rates of the egg and larval stages of these fish (Smith et al. 1994). For example, attempts to reestablish lake trout populations throughout the Great Lakes have been unsuccessful, largely because of the failure of the stocked lake trout to reproduce viable offspring rather than due to mortality of the stocked fish (Leatherland 1993: Smith et al. 1994). Embryos of coho salmon (Oncorhynchus kisutch) and chinook salmon (Oncorhynchus tshawytscha) from Lake Ontario were reared under hatchery conditions in 1990 (Smith et al. 1994). Smith et al. (1994) found that mean mortality rates were 46% and 24% which occurred prior to eye-up and from eye-up to hatch. However, the mortality rates did not correlate with either muscle or egg levels of total PCB, mirex, octachlorostyrene, or DDT (Smith et al. 1994). 2. 3. 7. 8-TCDD also did not
correlate with embryonic mortality (Smith et al. 1994). Smith et al. (1994) reported a number of other studies that also failed to find correlations between contaminants and embryo mortality in fish, thus suggesting that organochlorine compounds do not contribute significantly to embryo mortality despite the fact that dioxin-like compounds and organochlorines are abundant in chinook and coho salmon. They did however suggest that the failure to find such correlations between contaminants and mortality may be due to inappropriate analytical or bio-assays for measuring the activity of these compounds (Smith et al. 1994). The understanding of toxic contamination continues to evolve rapidly.

Exotics

Exotic species have made their way into Lake Erie through deliberate and unintended introductions. The first intentional releases came in 1870 when salmonines (coho salmon, chinook salmon and Atlantic salmon; brown trout and rainbow trout) and common carp were stocked by government fish hatcheries into the lake as an answer to low catch rates of the preferred species such as Atlantic salmon, blue pike, sauger, lake herring and lake whitefish (Hartman 1972; Mills et al. 1993). Only coho salmon, chinook salmon and brown trout established naturally reproducing populations (Hartman 1972).

The most probable modes of unintentional introduction of exotic species into Lake Erie is through shipping activities (offloading of solid ballast and ballast water) and canals (Mills et al. 1993). With the opening of the Welland canal in 1829, the Erie-Ohio canal
in 1832. and the enlargement of the St. Lawrence Seaway on June 26, 1959. entrance and establishment of exotic species in the Great Lakes. including Lake Erie. dramatically increased because larger ships were able to pass through the canals with greater frequency. and species present only in Lake Ontario could now move into the Upper Great Lakes (Mills et al. 1993). Ballast water or solid ballast from foreign water bodies was dumped into the lakes before these ships took on cargo. Exotics still make their way into Lake Erie. though efforts are made to limit transportation of exotics by requiring mid-ocean ballast water exchanges. by legal restrictions on intentional releases. and by ballast water inspections.

These exotics have continued to change the Lake Erie ecosystem. affecting the native fish mostly through competition and predation. Some exotics that have demonstrated substantial effects are sea lamprey (established 1921), chinook salmon (1873), alewife (1873), common carp (1879), brown trout (1883), coho salmon (1933), white perch (1950), ruffe (1986), and zebra mussels (1988) (Mills et al. 1993).

**Fishery exploitation**

Commercial fishing began in Lake Erie over 180 years ago. The lake sturgeon is the first example of a Lake Erie fish species decimated by humans. Caught in gillnets directed at lake trout. lake herring and lake whitefish. these huge fish readily tore the cotton or linen nets with their external bony armour (Hartman 1972; Regier and Hartman 1973). Fishermen considered sturgeon a nuisance fish and would destroy these fish by piling them up and burning them (Hartman 1972; Regier and Hartman 1973). Because this
species grows slowly and matures at 15-35 years of age. It did not take long to reduce the numbers of sturgeon (Hartman 1972; Regier and Hartman 1973). It was not until the 1960’s that fishermen saw the value (i.e. caviar and oil) of sturgeon, but by then it was too late (Hartman 1972; Regier and Hartman 1973). With the sturgeon greatly diminished, extensive fishing ensued for lake trout, lake herring and lake whitefish. Catches of these fish fluctuated for several decades being mostly supported by a few large year classes before catches became insignificant in the 1950’s. Commercial fishing then focussed on other fish species such as blue pike, sauger and walleye.

Fishing in the 1950’s intensified for a number of reasons: (1) new large markets opened up due to increased demand for fish from other countries. (2) there was a continued lack of restrictive regulations. and (3) the development of new fishing gear such as the nylon gillnet that did not damage as easily and was less visible than cotton. As a result, many fish species such as blue pike, sauger and walleye continued to decline to commercial extinction (Hartman 1972; Regier and Hartman 1973).

Moderate numbers of blue pike were captured in the fisheries from the late 1800’s to 1915 before year class strength and resulting catches fluctuated (Hartman 1972; Regier and Hartman 1973; Nepsey 1977; Koonce et al. 1996). Year class strength varied widely from 1915 to 1959 with the last strong year class produced in 1954 (Hartman 1972; Regier and Hartman 1973; Nepsey 1977; Koonce et al. 1996). Although recruitment remained low after 1954, catches remained high. High growth rates (associated with low population densities) led to the removal of younger, immature fish because they now met

In the mid-1930’s, walleye, a valuable commercial and sport fish in Lake Erie started to experience large fluctuations in yield. The patterns of walleye fluctuations were similar to those of the blue pike. There was a series of strong year classes from 1942-1952 and a series of weak year classes from 1953-1961: walleye catches began to collapse in 1957 (Hartman 1972: Regier and Hartman 1973: Nepsey 1977). The similarity between histories of walleye and blue pike suggests similar stresses were involved in the demise of both fish species by the early 60’s (Nepsey 1977).

Yellow perch in Lake Erie

Variability in catches and year class strengths

By the 1950’s and 1960’s, the lack of highly-valued marketable fish species such as blue pike, sauger, walleye, lake herring and longjaw cisco caused the fishing industry in Lake Erie to shift to the yellow perch stocks. Catches of yellow perch increased greatly, and were augmented further by the replacement of cotton nets with nylon ones (Regier and Hartman 1973). Coincidentally, a number of very strong year classes contributed to large catches in the late 1950’s and 60’s (Nepsey 1977).
Once fishing focused more on yellow perch, these percids experienced the same catch instability (possibly caused by overfishing and perhaps exacerbated by various perturbations like eutrophication, toxins and exotic species) as was seen in the earlier preferred species. Prior to intensified fishing, strong year classes occurred in alternate years (1952, 1954, 1956) (Hartman 1972; Nepsey 1977). Then the periods between strong year classes slowly increased (3 year cycle: 1959, 1962, 1965: 5 year cycle: 1965, 1970, 1975) (Hartman 1972; Nepsey 1977). The next dominant year classes did not occur until the early 80's (1982 and 1984) (GLFC 1998). Throughout the rest of the 80's and into the 90's, yellow perch experienced declines in adult abundance and a long period of low and inconsistent recruitment (Norton 1997: GLFC 1998). Yellow perch stock size, harvest and catch rates reached historic lows from 1991 to 1995 (Norton 1997: OMNR 1997: GLFC 1998). Recently there have been a few moderate year classes (1993 and 1994) and one very strong year class in 1996, despite the fact that CPUE (catch per unit effort) of adults has remained fairly steady since 1991 (GLFC 1998). Managers currently speculate that a combination of weather conditions lead to the large 1996 year class (Timothy Johnson, personal communication, Ontario Ministry of Natural Resources, Wheatley). The winter of 1995 was not very harsh while the spring of 1996 was warm and the following winter was mild. This combination of conditions may have led to better growing conditions during the summer months and low over-winter mortality, all of which may have contributed to better survival.
The history of growing instability led to increasing interest in year class strength variation in yellow perch. Yellow perch populations often exhibit large fluctuations (400 fold) in year class strength (Le Cren et al. 1977; Craig et al. 1979; Craig and Kipling 1983; Henderson 1985). According to the classic density-dependent stock-recruitment relationship, as the abundance of spawners declines, production of recruits per spawner should increase faster than the reduction in spawners over some intermediate density range because of a reduction in intraspecific competition. However, for percids, no statistically significant relationship between stock and recruitment has been found. Therefore, scientists sought a cause and effect relationship between year class strength and various abiotic (temperature, water levels, wind) and biotic (predation, cannibalism, interspecific competition) factors affecting early life history. Attempts to relate variation in year class strength to these environmental conditions are reviewed below.

**Abiotic factors**

**Temperature**

The most widely reported abiotic influence on year class strength (YCS) is temperature. Of the 6 studies reviewed, only 2 (Eshenroder 1977; Kempinger and Carline 1977) had sample sizes greater than 10 years (Table 1). Of those 2, Eshenroder (1977) used qualitative comparisons and provided no statistical analyses or raw data that would allow one to perform post-hoc analyses. Kempinger and Carline (1977), on the other hand, used statistics to show that daily spring warming rates were not significantly correlated with the density of fingerlings over a 15-year period. Of the remaining 4 studies, all of which had sample sizes less than 10 years, only half identified any pattern related to
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<td>Busch et al 1975</td>
<td>Lake Erie (25690)</td>
<td>Walleye</td>
<td>1966-1970 (11 but 2 years excluded from test because were very strong year classes)</td>
<td>Seasonal mean (April-May) # of YOY walleye caught per trawling hour</td>
<td>YOY</td>
<td>Mean daily warming rate from April 1 - May 15 (45 day period that includes spawning &amp; incubation)</td>
<td>Rate vs. index of YOY</td>
<td>r= -0.90 (n=9) with 2 years excluded p&lt;0.001</td>
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</tr>
<tr>
<td>Clady 1976</td>
<td>Oneida Lake, New York (2067)</td>
<td>Yellow Perch</td>
<td>1969-1975 (7)</td>
<td>Mark-recapture of adult stock for measurements of fecundity; (abundance of resulting cohort determined from annual larval surveys)</td>
<td>Eggs to larvae</td>
<td>Daily warming rates measured starting from 3 weeks preceding the day when population reached a mean TL of 8 mm</td>
<td>Warming rates with *survival from egg to 8mm larve</td>
<td>Not correlated strongly r=0.90, p&lt;0.02 n=7</td>
</tr>
<tr>
<td>Eshenroder 1977</td>
<td>Saginaw Bay Lake Huron (2960)</td>
<td>Yellow Perch</td>
<td>1957-1975 (20)</td>
<td>CPUE (trapnet)</td>
<td>Not clear</td>
<td>Rate of spring warming = °C warming for 30 days after water temperature reaches 10°C, divided by SE of daily warming rates</td>
<td>Qualitative comparison of spring warming index with YCS</td>
<td>Statistics questionable and data uninterpretable</td>
</tr>
<tr>
<td>Carlander and Payne 1977</td>
<td>Clear Lake Iowa (14.74)</td>
<td>Walleye</td>
<td>Not clear</td>
<td>Mean catches of walleye per gillnet hour</td>
<td>Various ages</td>
<td>Not stated</td>
<td>Rates of warming with YC abundance</td>
<td>No significant correlation (but no numbers)</td>
</tr>
<tr>
<td>Kempenrger and Carlino 1977</td>
<td>Escanaba Lake Wisconsin (119)</td>
<td>Walleye</td>
<td>1958-1972 (15)</td>
<td>Density #/ha from multiple mark and recapture methods</td>
<td>Fingerlings</td>
<td>Rates of warming during spawning and incubation Average daily temp for 30 days after ice-out</td>
<td>Daily warming rates with density of fingerlings</td>
<td>No r-value provided (specified probability value implies correlation coefficient should be &lt; 0.5)</td>
</tr>
<tr>
<td>Willemsen 1977</td>
<td>Lake IJssel Netherlands (1200)</td>
<td>Pikeperch</td>
<td>1966-1975 (10)</td>
<td>YOY pikeperch taken/trawling hour</td>
<td>YOY</td>
<td>Not stated</td>
<td>Correlations of summed degrees days above 14°C and YOY pikeperch CPUE</td>
<td>r=0.80 * p&lt;0.01 n=9 (after the removal of one data point)</td>
</tr>
</tbody>
</table>

* Willemsen (1977): degree days vs. YOY pikeperch with all data points yield r = 0.6255 (p>0.05, n=10)

Willemsen (1977) values for Eurasian perch (Perca fluviatilis) from the author's (T.T.) analyses are as follows—
degree days vs. YOY perch CPUE (r = 0.48, p>0.2, n=8); degree days vs. number of perch in catch (r = 0.82, p<0.05, n=7)
temperature. Carlander and Payne (1977) found no significant correlation between rates of warming and year class abundance, while Clady (1976) found that daily warming rates were not strongly correlated ($r_s = -0.50, p>0.20, n=7$) with % survival from the egg to 8mm larvae stage.

Two studies, both with sample sizes less than 10 years showed significant positive correlations between the CPUE of young-of-the-year (YOY) and temperature (Busch et al. 1975; Willemsen 1977). Willemsen (1977) correlated the number of degree days above 14°C with an index of YOY pikeperch and found the correlation coefficient value of 0.84 ($p<0.01, n=8$) which supported a temperature effect. The correlation between summed degree days and the number in the catch at the age of recruitment (age 2 for pikeperch; age 3 for perch) was also strong (pikeperch: $r=0.8, p<0.01, n=9$; perch: $r=0.82, p<0.05, n=7$) (Willemsen 1977). Busch et al. (1975) also observed for walleye a positive correlation between YCS and the rate of water warming from spring spawning to incubation.

Overall, then the evidence is conflicting. For the largest datasets there is no clear relationship with temperature alone. Smaller datasets sometimes show significant positive correlations, but the variable results may reflect the unreliability and lack of statistical power resulting from small samples of years. I used a meta-analysis to evaluate the strength of the combined evidence for temperature effects on perch YCS.
Procedure for meta-analysis

We considered the application of meta-analysis to aid us in the overall interpretation of the findings in these studies for several environmental factors. Meta-analysis allows us to combine statistics from a number of independent populations (where individually they do not yield useful information because of low power and where the probabilities of each test may be low enough to be suggestive, but none are sufficiently low to enable one to establish statistical significance (Sokal and Rohlf 1995) to arrive at more powerful generalizations about a variable’s relationship with year class strength.

To determine which studies would be included in the meta-analysis, we placed studies into several categories based on specific criteria. First of all, for a particular variable, only those studies in which similar hypotheses were tested were used in the overall analysis. Separate meta-analytic tests were performed if the hypotheses differed. The results of each group of studies addressing a single hypothesis were then classified into two categories: (1) Negative or heterogeneous groups: Groups that include one or more studies with statistically significant results in opposition to the hypothesized relation with perch YCS and (2) Consistent but individually inconclusive results: Sets of studies with no statistically significant results opposing the hypothesis, and with one or more results consistent with the hypothesis but not necessarily statistically significant. If, for a variable, studies were placed in category 1, then it was concluded that the data do not support the idea that such variables are consistently associated with year class strength. If all studies for a variable were placed in category 2, then a meta-analysis was performed. Fisher’s method was used to test the overall hypothesis. Details of the test
are given in Sokal and Rohlf (1995). Once an overall significance test was calculated, we then tested for homogeneity among the correlation coefficients using a test based upon Fisher's z-transformation (Zar 1984) only if the null hypothesis of no effect was rejected. If the coefficients are homogeneous, then a common correlation coefficient can be calculated. If not then subgroups of studies with differing levels of relationship must be present. We present results of a meta-analysis for studies on temperature effects on YCS of percids as well as studies on competition effects on the YCS of yellow perch.

Meta-analysis on temperature

The hypothesis that temperature is positively correlated with the YCS of various percids was tested (Appendix 1). Five separate tests (Busch et al. 1975; Willemsen 1977) were included in the meta-analysis. If a study included 2 different correlation coefficients calculated with and without the removal of extreme values, then the correlation coefficient corresponding to the whole dataset was used in the meta-analysis. The overall significance test in the meta-analysis resulted in a probability under the null hypothesis of 0.001, thus rejecting the null hypothesis and accepting that temperature is positively correlated with YCS. We also found that the coefficients were homogeneous and therefore we were able to calculate a common correlation coefficient which was r=0.54.

Wind

Wind is another abiotic variable frequently thought to affect YCS. Moderate winds are thought to be important to egg development by circulating oxygen needed by the eggs (Busch et al. 1975; Clady 1976). However, it is thought that very strong winds can
adversely affect eggs by displacing them onto beaches or into other unfavourable locations (Busch et al. 1975: Clady 1976). Busch et al. (1975) observed before a strong storm in May that many walleye eggs were found in cracks and crevices of the reef in Lake Erie, and that after the storm, no eggs were seen and were presumably displaced in the deeper, colder muddy bottom waters of the lake. However this was only a single observation. Studies of wind effects on YCS are summarized in Table 2. All studies had fairly small sample sizes (<11 years).

There has been some indication that wind and temperature act together. Changes in wind caused by storms can create internal seiches that cause thermal shocking (Newsome and Aalto 1987). Newsome and Aalto (1987) showed that a temperature change of as little as 2°C can inhibit or even kill eggs. G. E. Newsome (unpublished, as cited in Newsome and Aalto 1987) has shown that perch embryos which have been subjected to frequent thermal shocks of as little as 2 degrees are more likely (exactly how much more likely in quantitative terms was not stated) to result in hatch fry exhibiting abnormal gill and jaw development and smaller pectoral fins than is typical for embryos maintained at a constant or slightly rising temperature. Severe deformities lead to immediate death while less severe deformities will have a "significant" effect on survival of the perch at other critical life stages during the first year (Newsome and Aalto 1987).

A few studies examined the question of whether the strength of the wind alone or the wind velocity plus direction contributed to variations in perch numbers. Clady (1976) found a fairly strong ($r_s=-0.54$ to $-0.61$) but not statistically significant correlation
Table 2. A summary of studies of wind effects on the YCS of perchs

<table>
<thead>
<tr>
<th>Reference</th>
<th>Lake &amp; Lake size (km²)</th>
<th>Fish Species</th>
<th>Time period &amp; # of years</th>
<th>YCS Measure</th>
<th>Life Stage</th>
<th>Wind Measure</th>
<th>Test</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Busch et al 1975</td>
<td>Lake Erie</td>
<td>Walleye</td>
<td>1960-1970 (11)</td>
<td>Absence of eggs on reefs (qualitative)</td>
<td>Daily prevailing wind direction</td>
<td>Determined which days had a temperature reversal (decline) of 0.5 degrees or greater. Then observed for one day when a temperature reversal occurred</td>
<td>Concluded that wind had an effect on mixing the waters to cause a temperature reversal; they observed prior to that particular chosen day that eggs were visible on reefs and after the storm, eggs were presumably dispersed into unsuitable territories.</td>
<td></td>
</tr>
<tr>
<td>Clady 1976</td>
<td>Onunda Lake New York</td>
<td>Yellow Perch</td>
<td>1969-1975 (7)</td>
<td>* survival from egg to 8 mm larvae</td>
<td>Eggs to larvae</td>
<td>Mean wind (m/s) velocities per day for 4 weeks preceding the date of attainment of a mean length of 8 mm</td>
<td>* survival vs mean wind velocity</td>
<td>r= -0.61 p&gt;0.1 n=7</td>
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<td></td>
<td>*Note- a Bonferroni correction is appropriate here (between the 2 tests of mean wind and max wind), so the critical value should be 0.025</td>
</tr>
<tr>
<td>Newsome and Aalto</td>
<td>Lochaber Lake Nova Scotia</td>
<td>Yellow Perch</td>
<td>1978-1986 (9)</td>
<td>Annual census of perch egg masses to determine the number of adults from June 16-23 after termination of spawning</td>
<td>Sum of hourly mean velocities from 16 cardinal compass directions</td>
<td>Correlation of total wind velocities and annual variations in perch numbers</td>
<td>No significant relationship (no numbers provided)</td>
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<td></td>
<td>r=0.875 transformed from r=0.765 p=0.07 (for regression), n=9 borderline significant (but far from significant after a Bonferroni correction)</td>
</tr>
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</table>

suggest northerly winds may play an important role.
(p>0.1) between wind velocity for the month of June and survival from egg to the larval stage of yellow perch using 7 years of data. Newsome and Aalto (1987) also failed to find a significant relationship between total wind velocities (=sum of hourly mean velocities) and annual variations in perch numbers in Lochaber Lake, Nova Scotia. However, they did find a strong relationship between wind direction (northerly winds) for the month of June and an index of relative change in female abundance (r=0.875, p=0.07) (Newsome and Aalto 1987). It does not appear that explicit questions of the effect of certain wind directions on YCS were specifically being tested. In fact, they randomly selected sites around the lake and performed multiple tests. This would mean that a Bonferroni correction should have been applied to the critical alpha for these multiple tests to avoid inflating the Type I error rate. Thus, the correlation that they report may be a chance occurrence. In Oneida Lake, winds from most directions can generate significant internal circulation patterns (Clady 1976) whereas in Lochaber Lake, which is much narrower and deeper, only winds from specific directions would be capable of generating internal seiches (Newsome and Aalto 1987). In Oneida Lake, only winds from a northeasterly or southwesterly direction would be effective in generating "rocking" internal seiches (Newsome and Aalto 1987). Therefore, it is not only how strong the wind is, but also how the lake is situated in receiving the wind that would affect egg survival.

To summarize, wind studies on yellow perch recruitment are very sparse. The few existing data suggest that wind can affect YCS and lead us to expect that predictive models of its effect need to be lake specific, taking into account wind patterns and lake
orientation and morphometry. For Lake Erie, winds from the two prevailing directions (northwest or northeast) both have long fetches. Wind effects on Lake Erie are thus very likely. Along the shallower reefs where yellow perch spawn, strong winds from any direction can cause bottom turbulence and thus might affect eggs (Busch et al. 1975). However, there have been no quantitative attempts to relate wind records to YCS for perch in Lake Erie. Since there were too few relationships in the literature, a meta-analysis was not performed.

**Biotic factors**

**Predation**

Another determinant of dominant year classes of yellow perch is thought to be predation by walleye (Table 3). Walleye and yellow perch co-occur in many North American lakes and are thought to form a tightly coupled predator-prey species pair (Rudstam et al. 1996). Long-term studies on these 2 species in Oneida Lake have shown that when walleye are abundant, they are the main predator of young-of-the-year (YOY) yellow perch (Rudstam et al. 1996). If there is a tightly coupled predator-prey relationship, one might expect a negative correlation between growth rates of walleye and yellow perch (Rudstam et al. 1996). If abundant walleye populations limit density of YOY perch, the surviving YOY perch would grow well and their low density would produce slow walleye growth. Sparse walleye populations would allow for fast walleye growth and strong perch recruitment with high perch densities and slow perch growth. Rudstam et al. (1996) tested this predator-prey relationship by looking at age 4 walleye and yellow perch.
Table 3. A summary of studies of walleye predation on the YCS of yellow perch

<table>
<thead>
<tr>
<th>Reference</th>
<th>Lake &amp; Lake Size (km²)</th>
<th>Fish Species &amp; Predator</th>
<th>Time period &amp; # of years</th>
<th>Sampling of fish</th>
<th>Life Stage</th>
<th>Test</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nielsen 1980</td>
<td>Oneida Lake (206)</td>
<td>1 Walleye, 2 Yellow Perch</td>
<td>1962-1974</td>
<td>CPE on Oct 15 from trawls was calculated as an index of the abundance of age 0 perch</td>
<td>0, 1, 2 year olds</td>
<td>The intensity of walleye predation on age 1 and 2 perch was assessed from the frequency of occurrence of perch in stomachs of age 3 and older walleyes during May-Dec in 1967-1974</td>
<td>5-13% of 8743 walleye stomachs examined during 1967-74 contained few age 2 perch</td>
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<td>Abundance of age 1 perch on May 1 was estimated from mean CPE for the 2 spring trawling dates</td>
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<td></td>
<td>CPE of age 1 and 2 perch were estimated from seine data during July</td>
<td></td>
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<td>Instantaneous mortality coefficients: natural log of mean trawl catch at age 2 divided by mean catch at age 0</td>
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<td>Correlation between relative instantaneous mortality coefficients of perch cohorts b/w age 0 and age 2 compared with biomass of walleyes when perch were age 1 (May 1)</td>
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<td>Perch mortality coefficient vs. perch YOY density on Oct. 15</td>
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<td>Perch mortality coefficient (age 0-2) vs. density of following perch cohort (age 0 perch of following cohort on Aug 1)</td>
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<td></td>
<td>Perch mortality coefficient (age 0-2) vs. lengths of perch age 0 (Oct 15) and age 1 (Sept 1)</td>
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<tr>
<td>Rudstam et al. 1996</td>
<td>Various NY lakes 23 in total</td>
<td>Walleye, Yellow Perch</td>
<td>Various years</td>
<td>Age 4 walleye, Age 4 yellow perch</td>
<td>Mean length at age 4 walleye vs. mean length at age 4 yellow perch</td>
<td>r = -0.45 transformed from r²=0.201, N=90 (multiple years for some lakes), p&lt;0.001</td>
<td></td>
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<tr>
<td>Hartman and Margraf 1993</td>
<td>Lake Erie (25690)</td>
<td>Walleye, Yellow Perch</td>
<td>1988</td>
<td>Walleyes collected twice monthly from June to Oct 1988 by bottom trawling</td>
<td>0, 1, 2 walleye, age 0 yellow perch</td>
<td>Modeled consumption of yellow perch by walleye over a 60 day period</td>
<td>Estimated small walleye age (0-2) are about 28% of young yellow perch during June and July 1988</td>
</tr>
<tr>
<td>Fornay 1971</td>
<td>Oneida Lake (206)</td>
<td>Walleye, Yellow Perch</td>
<td>1959-1968</td>
<td>Abundance of young perch estimated each year from shore seineing in early summer and by trawling in late summer and fall</td>
<td>Age 0- and 1- yellow perch</td>
<td>Compared mean number of YOY yellow perch caught in seine hauls over years</td>
<td>3-fold among-year variation in population density of YOY yellow perch in early July (time when YOY yellow perch become pelagic) increased to 70-fold at age 1-</td>
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<td>Compared relative abundance of the 1959-67 year classes of yellow perch estimated from seine and trawl catches at 0- and 1-</td>
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</tbody>
</table>

23
Perch mortality coefficients from Aug 1 to Oct 15 vs. indices of perch abundance from trawl catches on Oct 15 and seine catches in July.

Perch mortality coefficients between Aug and Oct vs. biomass of yellow perch on Aug 1.

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Species</th>
<th>Period</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>Oneida Lake</td>
<td>Walleye</td>
<td>1971-1973</td>
<td>Daily consumption of age-0 yellow perch by walleye was estimated from the number of young observed in stomachs Walleye were captured by bottom trawls Abundance of young YOY perch were estimated in early June from the catch in Miller samplers at 42 sites Age 1-5 walleye, Age 0 yellow perch Cohorts of young perch were reconstructed by adding to the number remaining in Oct. the number eaten by walleye and adult perch in preceding weeks Daily instantaneous mortality coefficients = slopes of regressions fitted to natural logarithms of trawl catches of perch from July to October</td>
</tr>
</tbody>
</table>

For each year 1971 to 1973, the reconstructed cohorts approached or exceeded the number in early June estimated from the catch in Miller samplers

<table>
<thead>
<tr>
<th>Year</th>
<th>Miller Sampler June</th>
<th>1971</th>
<th>1972</th>
<th>1973</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>240 000</td>
<td>216 000</td>
<td>17 000</td>
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<tr>
<td></td>
<td></td>
<td>79 000</td>
<td>121 000</td>
<td>17 000</td>
</tr>
<tr>
<td></td>
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<td>17 000</td>
<td>17 000</td>
<td>17 000</td>
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</tbody>
</table>

perch in 23 different water bodies in the upper New York state. They found a significant negative correlation between walleye length at age 4 and yellow perch length at age 4 in these lakes. This is consistent with walleye having an effect on yellow perch YOY populations across a wide range of lakes (Rudstam et al. 1996), but might also arise if walleye grow best in a different kind of lake than perch do. Although the regression was significant, it only explained about 20% of the variation ($r^2=0.2$, $N=90$ (included multiple years from some lakes), $p<0.001$) and thus would indicate that walleye may not be the dominant factor influencing yellow perch year class strength (Rudstam et al. 1996).
Although walleye predation will have a negative effect on survival of perch (Nielsen 1980 and Hartman and Margraf 1993), the valuable question is whether this predation controls perch year class strength through variable yearly mortality of perch. Several studies that evaluated the predation hypothesis in Oneida Lake resulted in different conclusions. The first study involved looking for negative relationships between walleye densities and perch mortality. Nielsen (1980) found that over a 12-year period in Oneida Lake, New York, there was no apparent relationship between YOY perch mortality and walleye density. In fact, walleye densities remained relatively constant and Nielsen suggested that rates of predation on 1+ perch were modified by perch length, perch cohort density and density of the following age-0 perch (alternative prey for older perch i.e. cannibalism). He found a significant positive correlation between perch mortality rate (from age-0 to age 2) and that cohort’s density at age-0 suggesting intraspecific competition determines mortality of young perch (Nielsen 1980). Intraspecific competition should result in size differences between perch cohorts, and if predation is a principal cause of mortality and walleye are size-selective predators, the length of perch should also be negatively related to predatory mortality rates. In fact, Nielsen (1980) found a significant negative correlation between mortality rate of perch aged-0 to age 2 and that cohorts length at the end of the first summer at age 0 and at age 1. This suggests that fish that grew faster were less susceptible to mortality from predation or died from competition, given that the slower growing ones also had higher densities. Furthermore, he found a negative correlation between mortality rate (age 0 to 2) and the density of the following perch cohort (age 0) and suggested that this reflected a dependence of 1+ and 2+ perch on 0+ as prey. These results suggest that the abundance of perch cohorts are
determined principally by density-dependence within perch cohorts and only secondarily by walleye predation.

In another study of Oneida Lake, predation-generated depensatory mortality was suggested as the principal factor in contributing to the development of dominant year classes of yellow perch. This claim is very different from Nielsen's conclusion that walleye do not control perch numbers. Forney (1971) found that perch mortality rate was higher in years when the abundance of perch in late summer was low, indicating that walleye took a higher proportion of small year classes and a lower proportion of initially large year classes. The same negative correlation was found between mortality of YOY and YOY perch biomass, although both correlations were nonsignificant (Forney 1971). Predation may have a depensatory effect on year class abundance when the growth of prey (i.e. perch) is not strongly density-dependent. Forney (1971) suggested that the differences in the size of perch in years when density appeared similar suggested that growth of perch was not strongly density dependent. Therefore, numerically large year classes would tend to attain the highest biomass and a smaller proportion of this biomass would be required to satisfy the needs of the walleye population than that required from small perch year classes with low biomass. Therefore, he concluded that mortality decreases with increasing density and suggested that predatory mortality by walleye was predominantly a depensatory effect on year class abundance after perch became benthic (Forney 1971).
In a 1977 paper, Forney examined the pattern of mortality and changes in abundance of young yellow perch during the first year in life. He reconstructed cohorts of yellow perch in Oneida Lake from the examination of predator stomachs. He determined that predation by older walleye (age 1-5) and to a lesser extent adult yellow perch did account for most of the loss of young perch between June and October. From reconstructing the perch cohort, he found that the number of age-0 perch consumed by walleye and adult perch added to the number remaining in October approximately matched the young available in June that were estimated from the catch in the Miller samplers (Forney 1977). He also discovered that the populations constructed from estimates of numbers of perch consumed and the estimates from trawl catches both showed the same steady exponential decline from June to October which suggested a fairly constant mortality rate and the rates differed between years (Forney 1977). From the 3 years of data looked at in this particular study, he found perch mortality in 1971 was low when perch were abundant and in 1972 perch mortality was high when perch were scarce. However, mortality of perch was low for the 1973 year class despite low perch density. He attributed this to a fairly large decline in walleye biomass (Forney 1977). Forney (1977) found that the data from these few years was generally consistent with the concept that mortality rates were higher at low perch densities and supported his earlier conclusion that walleye predation was depensatory. although no statistical analyses were performed on the combination of these few years of data with data from his earlier study (Forney 1971). Thus, it seems to be a very subjective a priori interpretation of just a few years of data. He had an “a priori” hypothesis based on his 1971 study and found that it was
consistent with 2 of the 3 years of data and that the exception had an explanation that was consistent with the proposed mechanism.

Once again, a meta-analysis could not be performed on these predation studies because of the wide range of ways at looking at predation effects. However, overall, the results of these studies, especially those performed on the same lake (i.e. Oneida Lake) have resulted in conflicting interpretations of walleye predation on yellow perch YCS. But it seems that both Forney (1971) and Nielsen (1980) agree that walleye predation does not stabilize perch numbers but intraspecific relationships might. Although Forney (1971) concluded that depensatory mechanisms shaped the YCS of perch, he suggested that this mechanism only occurred when the growth of perch was not strongly density-dependent. Nielsen (1980) determined that within perch cohort density-dependence and subsequently predation by walleyes are responsible for shaping the YCS of perch (Nielsen 1980). As suggested by Nielsen (1980) predation may not be the primary factor regulating YCS and it may result only after other factors have come into play such as temperature effects on growth rates and hence the time in which perch stay in the vulnerable size range.

Interspecific competition of yellow perch with other fish species over a limiting food source could result in one or both of the fish species to grow slowly thus making them also vulnerable to predators. This suggests that Rudstam's (1996) interlake pattern might not be generated by walleye control of perch abundance.

As for walleye and yellow perch in Lake Erie, it might be expected that in recent years walleye has had little impact on yellow perch for several reasons. In Lake Erie where
both walleye and yellow perch stocks are heavily exploited. Both populations would have low density (walleye more so than yellow perch since walleye have a high market value) and thus the encounter rates of predator to prey would be relatively low. These encounter rates can depend on the degree of clumping of prey and the abilities for predators to find where prey concentrations are. Quotas of walleye have been declining throughout the 1990's. With the reduced yellow perch stocks throughout the late 80's and 90's, the growth rate of these fish would be expected to be faster (which has been observed Norton (1997)). Thus yellow perch would grow out of the vulnerable stage faster and therefore be less likely to be preyed upon by walleye. There is evidence in Lake Erie that predation by walleye does not exist any longer. In a recent extensive lakewide diet study on walleye found that walleye do not eat yellow perch (Tim Johnson, personal communication, OMNR, Wheatley). In all basins of Lake Erie over the past 10 years, walleye diets have been mostly comprised of clupeids, cyprinids and smelt. Perhaps then, the several papers on walleye predation on perch in Oneida Lake are not very useful for the situation in Lake Erie. Thus overall, walleye does not currently appear to have a negative effect on yellow perch in Lake Erie.

**Competition**

Competition from white perch is yet another possible influence on year class success of yellow perch (Table 4). Competition between the two species provided a possible explanation for the poor recruitment success of yellow perch since the two species shared similar prey and spawning habitat and most importantly, the increase in white
Table 4. A summary of studies on yellow perch competition with white perch and the effects on the YCS of yellow perch

<table>
<thead>
<tr>
<th>Reference</th>
<th>Lake &amp; Lake size (km²)</th>
<th>Fish</th>
<th>Time period (# of years)</th>
<th>Sampling of fish</th>
<th>Life Stage</th>
<th>Test</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parrish and Margraf 1980</td>
<td>Lake Erne</td>
<td>White perch</td>
<td>1983-85, 87 (3)</td>
<td>Bottom trawls on alternate weeks from May to Nov</td>
<td>Age 1 &amp; 2 White perch &amp; Age 1.2.3 Yellow perch</td>
<td>Looked at daily consumption rates and diet overlap of white perch and compared to yellow perch</td>
<td>In spring 1987, median amounts of food in white perch stomachs were approx. 16-58% greater than in yellow perch but food amounts at only 4/9 times differed significantly (Wilcoxon sign rank, p&gt;0.1)</td>
</tr>
<tr>
<td>Prout et al. 1990</td>
<td>Oneida Lake</td>
<td>White perch</td>
<td>1977-1987 (11)</td>
<td>Collected weekly from bottom trawls from mid-July to mid-Oct</td>
<td>Age-0 White perch &amp; Yellow Perch</td>
<td>Diet and growth compared b/w white perch and yellow perch</td>
<td>In 1980, diet overlap exceeded (Schoener index &gt; 0.6) from Aug to Oct, when daphnids were abundant</td>
</tr>
<tr>
<td>Norton 1997</td>
<td>Lake Erne</td>
<td>White perch</td>
<td>1977-1996 (20)</td>
<td>Trawling for young-of-the-year gillnets for adults</td>
<td>YOY &amp; Adults White perch &amp; Yellow perch</td>
<td>Recruitment</td>
<td>No correlation between indices of abundance of YOY yellow perch and white perch (r=0.35, df=13, p=0.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yellow perch</td>
<td></td>
<td></td>
<td></td>
<td>Growth vs Abundance (Intraspecific competition)</td>
<td>No correlation between yellow perch recruitment (YOY) and adult white perch abundance (r=0.04, df=12, p=0.8)</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>Growth vs Abundance (Intraspecific competition)</td>
<td>Size of yellow perch at age 3 and 4 were inversely related to their own abundance (West central age 3 ( r = -0.44, df = 17, p = 0.071 ), West central age 4 ( r = -0.58, df = 17, p = 0.015 ))</td>
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<td></td>
<td>Growth vs Abundance (Intraspecific competition)</td>
<td>Growth of white perch was inversely related to the abundance of white perch adults in the west basin (age 3 ( r = -0.44, df = 11, p = 0.13 ), age 4 ( r = -0.59, df = 8, p = 0.072 ), YOY ( r = -0.53, df = 14, p = 0.035 )) but not the west central basin (age 3 ( r = 0.32, df = 10, p = 0.31 ), age 4 ( r = -0.16, df = 5, p = 0.73 ))</td>
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<td></td>
<td>Size of yellow perch at age 3 and 4 were not negatively correlated with the abundance of adult white perch in either the West basin: (age 3 ( r = -0.22, df = 17, p = 0.38 ), age 4 ( r = 0.27, df = 17, p = 0.28 )) or West central basin: (age 3 ( r = -0.17, df = 17, p = 0.49 ), age 4 ( r = -0.19, df = 16, p = 0.46 ))</td>
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<td></td>
<td>Size of YOY yellow perch in Aug. was not negatively correlated with the abundance of adult or YOY white perch (adult: ( r = 0.11, df = 12, p = 0.57 ), YOY: ( r = 0.34, df = 13, p = 0.06 ))</td>
<td></td>
</tr>
</tbody>
</table>
perch roughly coincided with the decline in yellow perch recruitment (Schaeffer 1984; Schaeffer and Margraf 1986). Parrish and Margraf (1990) and Prout et al. (1990) both looked at diet overlap between white perch and yellow perch. Although there were similarities in the diets of adult and YOY white perch and yellow perch ((Elrod et al. 1981: Schaeffer and Margraf 1986) as cited in (Prout et al. 1990)). diet overlaps were only statistically significant approximately 50% of the time (Parrish and Margraf 1990) and the highest diet overlaps occurred usually when daphnids were abundant in mid-July (Prout et al. 1990: Wu and Culver 1994). In fact, large populations of young-of-the-year yellow perch can collapse *Daphnia pulex* populations and that can have greater effects on white perch YOY growth than large cohorts of YOY white perch have on yellow perch YOY growth (Prout et al. 1990). This reverse competition may be due to differences in the timing of resource use where yellow perch get to the resource first. Prior to the peak in the daphnid population in mid-July, yellow perch fed mostly on benthos and some fish. Once the daphnid population declined, both yellow perch and white perch sought other prey, which might have caused the slight but non-significant growth differences between the two species after the mid-summer period in both Oneida Lake and Lake Erie but overall this did not greatly limit yellow perch growth (Parrish and Margraf 1990).

Therefore, interspecific competition between white perch and yellow perch is very limited and exists only if a specific prey (e.g. daphnids: needed for the growth of YOY fish) is limited for both fish species.

If there were significant interspecific competition then one would expect to find negative relationships between recruitment of yellow perch and abundance of YOY white perch.
As well, the growth of YOY or adult yellow perch should be inversely related to the abundance of YOY or adult white perch. Norton (1997) found no correlation between yellow perch recruitment and YOY white perch abundance over 15 years in Lake Erie. Instead he found that the growth of YOY perch improved during the period of increasing white perch abundances. In fact, he found that the sizes of both yellow perch and white perch age 3 and 4 were inversely correlated with their own abundances in the west basin of Lake Erie, reinforcing our earlier suggestion that intraspecific competition may be more significant than interspecific competition (Norton 1997). He did find a negative relation between the size of YOY yellow perch and the abundance of adult white perch (although the mechanism for this is not known) but not for YOY white perch (Norton 1997). A meta-analysis was performed to test whether there was a negative relationship between the growth of yellow perch of various ages (YOY, age 3 and age 4) vs. the abundance of adult and YOY white perch across the basins in Lake Erie existed (Appendix 2). We found that there was no significant negative relationship between yellow perch and white perch. As more is known about the life history of white perch and its interactions with yellow perch, evidence is mounting that white perch and yellow perch are not as closely competitive as once thought, especially for yellow perch in Lake Erie as indicated by Norton's 20 year study. This is not to say that competition does not exist anytime, but that it is relatively unimportant and probably occurs during a limited time period. Thus, we can conclude that further studies on the interactions between white perch and yellow perch are not required.
Final thoughts and future research needs

Multivariate analyses

Attempts to correlate environmental factors with YCS have generally been unsuccessful. One possible reason for this has been because all of these studies only focussed on one variable to explain the variation in YCS. The environment of a fish is comprised of many varying factors. To expect that only one of those factors overrides all others in shaping the final year class of a cohort is unrealistic. The time to recruitment to the adult population may occur after 1 year or after many years. Generally for yellow perch in Lake Erie, a year class would first recruit to the fishing gear at age 2 with most of that year class recruiting at age 3. In such a long period of time between the egg stage and adulthood, many environmental factors can interact with each other or factors working in a sequence can mutually affect the outcome of the final cohort. The ultimate YCS is probably a result of many different factors interacting with one another. Therefore, the future direction in the study of environmental variables on YCS should be to include multivariate analyses: testing the interactions of both abiotic and biotic variables simultaneously. Since the studies on the effects of environmental factors on YCS lend themselves to be tested by correlations, a multiple correlation or regression technique would help incorporate several independent variables and their combined effect on the dependent variable. Another method that groups variables according to the magnitudes and interrelationships among their correlations is known as cluster analysis. Cluster analysis groups variables that are highly correlated with each other and excludes from a cluster those that are not. Below are some situations where interrelationships between environmental factors should be taken into consideration in future studies.
Both wind and temperature can interact with each other. More studies need to look at thermal shocking and its effect on the survival of eggs and the resulting larvae. In many of the studies reviewed here, temperature reversals caused by wind were observed during spring warming. However, there is no evidence that these temperature reductions are detrimental to the eggs and larvae. Research is needed to determine the tolerance limits of perch eggs to temperature reversals and their effects on the mortality of a cohort.

Although we know that very strong winds can be detrimental to eggs by displacing them to unfavourable locations. low wind speeds should also be considered here too. A personal observation of yellow perch spawning in the spring of 1998 led me to consider this idea. Although the typical time frame of spawning times for yellow perch in North America ranges from early April to mid-June (Craig 1987), yellow perch in Lake Erie spawn in the month of April, usually during the middle two weeks of the month. In 1998, yellow perch spawned a full month later, near the end of May. That spring was unusually calm and very hot, probably setting up the thermocline prior to the spawning period. The reason for delayed spawning may include the following. Some wind is important for the development and survivability of eggs by allowing the circulation of oxygen around the eggs. However, extremely low wind speeds can affect the thermal stratification of the water column of lakes. This in turn can affect the adult female’s ability to spawn eggs. One of the cues required to lay eggs for percids is a rising water temperature regime. Those years with low wind speeds would result in a shallower epilimnion and metalimnion which in turn could delay the spawning of eggs since the warm temperatures
would not penetrate to the depths preferred by females. Yellow perch have been observed to spawn at depths of 6-12 metres (Craig 1987; Newsome and Aalto 1987). If spawning is delayed for too long, eggs may become atretic and/or total reabsorption affecting YCS (Craig 1987).

Wind speed would also interact with the productivity of the lake. In oligotrophic or mesotrophic lakes, low wind speeds would not be a problem. While for eutrophic lakes with high sediment oxygen demand, calm periods could be lethal. High winds may also cause the resuspension of toxins that have settled out of the water column leading many organisms including fish to ingest such materials inadvertently and where toxic contaminants are known to have adverse reproductive effects (MNR 1985; Leatherland 1993).

Growth rates of yellow perch during the first year of life have been identified as critical in modifying mortality (e.g. vulnerability to predation and overwintering mortality) and recruitment in YOY fish (Miller et al. 1988; Post and McQueen 1994). Warmer temperatures favour faster hatching rates and higher growth in the larval stage thus allowing fish to achieve the size required to make the switch from endogenous to exogenous feeding (Hokanson 1977; Craig 1987). This faster growth allows these fish to feed on their preferred prey resource earlier in the year. Assuming the necessary food is available, the warmer temperatures and the shift in feeding allow these fish to develop faster, growing more quickly out of the vulnerable size range in which predation by piscivores may occur. In contrast, Post and McQueen (1994) found that prey availability
explained almost 93-98% of the variability in the growth of YOY perch while temperature showed no explanatory power although they suggested that the temperature range in their study was small and they expected that a much wider range in temperatures would affect growth rates. This latter study indicates that additional studies are important to understand intercohort growth dynamics.

Another indication that additional studies on within cohort dynamics are needed is shown by the evidence from the studies on predation and interspecific competition. These studies revealed that intraspecific competition within perch cohorts (modified by abiotic variables) may be the first determining factor affecting the variation in perch YCS, followed by other factors such as predation or competition.

**Length of studies**

The greatest improvement in all future studies would be to consider an extended time scale of study. In the studies reviewed here, the number of yearly values involved in correlations were generally under 10. At least 30 years of data would be required if a true correlation coefficient of 0.5 is to be detected at the 0.05 significance level with a 80% power. However, a sample size of 64 years would be needed for a correlation coefficient of 0.5 with the desire to reject the null hypothesis 99% of the time at the 0.05 level of significance (Zar 1984). To obtain this many years of data is unreasonable and unattainable. A statistical method that allows us to combine statistics from a number of studies and thus could aid us in the overall interpretation of the findings in these studies is the use of meta-analysis. We presented some of those results for both temperature and
competition. However, one particular hurdle we encountered in doing a meta-analysis is that similar hypotheses must be tested across the various studies inorder to able to combine them. If that prerequisite is met, then a meta-analysis is a powerful way to combine a group of individually weak datasets to make a much stronger statement about relationships. However, a meta-analysis that looks at correlation coefficients does not take into consideration the sample sizes of the individual tests. In effect, a meta-analysis may include several studies that have found a strong positive correlation with only a few years of data while there maybe only one study that found no significant positive correlation with many years of data. Since only the p-values are considered in the meta-analysis, the overall result would probably be skewed in the direction of the fewer years of data with significant p-values. This is a function of the type of studies actually published. There is a bias towards only publishing significant results which may limit the quality of a meta-analysis on a particular subject. A meta-analysis should take into account the individual sample sizes and weight the individual studies according to the sample size of the studies. An additional problem maybe the use of including more than one type of species. In particular, we combined data among a number of different percids species in the temperature analysis. It is unknown if the different life histories of the species may affect the overall result of the meta-analysis. This should be thoroughly evaluated in any future meta-analyses. Overall, multivariate studies over a long time period might greatly improve the predictions of year class strength in percids.
Goals of this thesis

It is evident from the review that none of the various mechanisms that has previously been thought to influence perch YCS has been shown in the literature to be a powerful and consistent influence. It appears that Clady (1976) was correct when he suggested that no major mortality factor but rather a complex interaction of many factors is responsible for annual variations in perch numbers.

The notion that maternal factors can influence viability of young and hence the number of successful recruits has not been considered for yellow perch. Forney (1971) indicated that year class size is determined ‘initially’ by the number of eggs spawned and subsequently by mortality. Marteinsdottir and Thorarinson (1998) and Scott et al. (1999) also asserted that the number of eggs spawned is determined by various factors associated with the female, such that the condition and size of the adult female can affect not only the number of eggs but also the size and condition of eggs and larvae. Henderson and Nepszy (1994) (who looked at the energetic condition of walleye in Lake Erie) suggested that the potential recruitment from a spawning stock may depend upon the energetic condition of the females and that the condition of these potential spawners may also determine what proportion of the female spawning stock actually goes on to reproduce. Only those females with an energetic surplus that could meet the requirements of reproduction would contribute to the spawning stock and to fecundity for the next year class (Henderson and Nepszy 1994). Henderson and Nepszy (1994) inferred that strong year classes may result when a high proportion of potential female spawners actually spawn. Studies on various northern fish species have shown that when there is a lack of
food in the environment. adult fish may skip a reproductive event (Diana 1983: Burton and Idler 1984: Pulliainen and Korhonen 1993: Adams and Huntingford 1997: Berg et al. 1998: Jonsson and Jonsson 1998). Presumably, such fish were not able to accumulate enough energy during a critical time of the year to allow them to develop a gonad. With these ideas in mind, the goals of this thesis are:

(1) to determine whether skipping reproductive events occurs among female yellow perch in Lake Erie and whether it translates to variations in year-to-year recruitment.

(2) if yellow perch are skipping reproductive events, we then want to determine the causes of yearly variations in the proportion of female yellow perch that mature and reproduce.

(3) Lastly, to model the effects of yearly variation in the proportion mature and other female reproductive parameters in the calculation of the stock in the stock-recruitment relationship.
References


Schaeffer, J. S. 1984. The white perch of Lake Erie: the ecology of an invading species. Columbus, OH. The Ohio State University.


Chapter 2:

Temporal variation in the fraction of the adult female yellow perch (*Perca flavescens*) reproducing in western Lake Erie
ABSTRACT

Over a period of 13 years, the proportion of adult female yellow perch actually reproducing in a given year varied from 0% to 18% for 2 year olds, 40% to 90% for 3 year olds, and 60% to 100% for age 4 fish. To determine what may be causing this large variation, we sought relations between the proportion of adult fish reproducing and the length of the fish, the previous year’s growth rate, and the condition of the fish. We found that for age 2, 3, and 4 year old fish, the average length at age was positively correlated with the proportion reproducing. Size at age was determined mostly by growth in the first 2 years of life. Growth rates in the third and fourth years of life were not correlated with the percentages of fish spawning at the end of those years. Condition of fish in a particular length range was significantly related to the proportion spawning only for the smallest size range of adults.
INTRODUCTION

Variability in recruitment has been identified as a central problem in fisheries research (Sissenwine et al. 1988). Fish recruitment can be affected by various abiotic and biotic factors, such as water temperature, water levels, wind, predation, cannibalism and competition. The age at maturity and the size of the spawning stock are also considered to affect recruitment (Sissenwine et al. 1988). According to the classic Ricker curve, recruitment is a function of spawning stock size (Craig 1987). For many fish stocks around the world, including yellow perch (*Perca flavescens*) in Lake Erie, there exists a high level of 'noise' around the stock-recruitment relationship. Most current research on recruitment variability assumes that stock (the number of adult fish) can be correctly estimated from age-specific catch per unit effort (CPUE) data, in conjunction with a fixed maturation schedule determining age at maturation. Maturation is often assessed in the fall, more than 6 months before the next spawning season, at a time when the appearance of the gonads may not be a highly reliable predictor of spawning readiness in the following spring. It is usually assumed that once a fish has reached the age of maturity, reproduction will be annual. If this assumption does not hold, the actual number of spawning females could differ among years even if the number of fish of reproductive age is constant. Such variation in the number of mature fish actually reproducing could be an unrecognized contributor to variation in recruitment and year class strengths.

Intermittent spawning has been most frequently documented in anadromous northern fish species such as Arctic charr (Dutil 1986; Jorgensen et al. 1997). Atlantic salmon (Whalen and Parrish 1999) and coregonines (Morin et al. 1982). These northern fish species live
in high-latitude environments characterized by substantial seasonal fluctuations in climatic conditions and food availability (Jorgensen et al. 1997). Anadromy may have evolved in these fishes as a means to take advantage of the favourable feeding conditions in the ocean, in locations where freshwater conditions for feeding and growth are poor (Dutil 1986; Jorgensen et al. 1997). For example, Arctic charr in the Nauyuk Lake system in the Northwest Territories, Canada (Dutil 1986) and Halsvassdraget water course in northern Norway (Jorgensen et al. 1997), can be subdivided into spawning and non-spawning substocks in any given year. Fish that reproduce in the spring remain in the freshwater over the summer and will lose approximately 80% of their body lipids from spawning and overwintering. They consequently do not spawn the next spring (Jorgensen et al. 1997). The second substock consists of adult, but non-spawning anadromous Arctic charr, who undertake a migration to the ocean in early summer. They reside in the ocean for 40-50 days and then return to the freshwater. During their short stay in the ocean, their body weight doubles and their body lipid concentration increases substantially (Jorgensen et al. 1997). Only the adult non-spawners migrate to the ocean in summer to feed (Dutil 1986; Jorgensen et al. 1997). Over the next winter, these migrating fish lose 30% of their body lipids from over-wintering and go on to spawn the next spring (Dutil 1986). Both Dutil (1986) and Jorgensen et al. (1997) concluded that the severity of the energy depletion prevents females from spawning in successive years. Several studies on Arctic charr and Atlantic salmon parr have shown that if an individual fails to exceed a threshold level of stored fat during a critical time of the year, the maturation process is switched off (Dutil 1986; Rowe et al. 1991; Simpson 1992; Jorgensen et al. 1997). Recently, Henderson and Nepszy (1994) suggested that walleye
in Lake Erie (a temperate environment) are not spawning in consecutive years and that the energetic condition of the spawners determines the proportion of the adult female stock that actually spawns. Bull and Shine (1979) suggested that low food levels are the cause of many iteroparous animals including fish species failing to spawn annually. Our primary objective is to determine if intermittent reproduction characterizes female adult yellow perch in Lake Erie. and if so, to determine if this variation of maturation is an important component of recruitment variation of yellow perch.

Our second objective is to determine if the variation in the proportion of mature female yellow perch after first maturation is a function of size and growth rates. It has been long known that variation in growth can affect the spawning stock size by changing the age at first maturation (Trippel 1995). However, very little information exists on spawning in successive years after first maturation has been reached. We assess whether successive spawnings by adult fish are a function of growth and, in particular, growth rates in the year prior to a given spawning.

Condition (i.e. fatness) has also been linked to the onset of gonadal development. Simpson (1992) and Bohlin et al. (1994) suggested that the rate of acquisition of surplus energy (measured as fat content of the fish) may influence the decision to spawn. Rowe et al. (1991) concluded that adequate fat levels are a prerequisite for hormonal triggering of sexual maturation. They also concluded for Atlantic salmon parr. that an internal decision to suppress maturation depends on the levels of body fat achieved during a 'critical period'. A low level of fat during this critical period apparently inhibits gonadal
recrudesence, causing interrupted reproduction. Our third objective is therefore to determine if body condition can explain the interannual variation in the proportion spawning among adult female yellow perch.
MATERIALS AND METHODS

Sampling

Samples of yellow perch were collected in multi-mesh, bottom-set gillnets set overnight in the Canadian waters of the west (82°30'-83°25'W) and west central (81°30'-82°30'W) basins of Lake Erie monthly in the spring (May-July, 1978-1990) (Norton 1997). Spawning in Lake Erie usually occurs in mid-April up to early June. All net gangs consisted of 50m panels of 51, 57, 64, 70, 76, 89, 102, 114 and 127mm stretched measure mesh (Norton 1997). Age (determined from scales), fork length, total length, round weight, sex and maturity were recorded for each fish. Several hundred fish were sampled each month. Most yellow perch were 2 to 5 years old.

Maturity assessment

Maturity of females was assessed by visual inspection of the size and colour of the gonad. Based on this inspection, fish were assigned to 1 of 5 categories: immature, developing, mature (developed), ripe and spent. Gonad appearance associated with each category (Treasurer and Holliday 1981) is as follows:

Immature: Small thread-like transparent organ lying underneath the bladder: no oocytes visible

Developing: Ovary is opaque and reddish with blood capillaries: occupies about half of body cavity: eggs visible to the eye are whitish and granular

Mature: Ovary fills ventral cavity: eggs completely round and only appear translucent a few days prior to spawning.

Ripe: Roe runs with slight pressure: most eggs translucent with few opaque eggs
left in ovary.

Spent: Ovary empty, flaccid and red, occupying about two-thirds of the body cavity; ovary wall thick and tough: a few residual oocytes may be visible

*Calculation of proportion mature*

The proportion female yellow perch classified as mature for a particular age, month and year was calculated by dividing the numbers of fish categorized as developing, mature (developed), ripe and spent, by the total number of female fish surveyed for that age, month and year. Proportions mature were arcsine-square root transformed before statistical analysis.

*Reliability of estimates of proportion mature*

In the determination of proportion mature, errors could arise from a) subjective human classification of maturity, b) errors in aging and c) non-representative sampling of the fish population. One way of evaluating the importance of these errors is to compare the temporal patterns across years in the proportion mature for samples made in May, June, and July (Figure 1).

We expected that the proportion mature would increase from May to July because all net sets were widely distributed and focused away from the spawning grounds. If the population of yellow perch segregates spatially into spawning and non-spawning females where the spawning females would be found on the spawning grounds then our May net locations would sample the non-spawning subpopulation. In June and definitely by July.
Figure 1. Interannual and between month variation in the estimated proportion of mature (reproducing) female yellow perch for age 2 (a), age 3 (b), and age 4 (c) fish in western Lake Erie. All proportions were calculated separately for the months of May (open circles), June (open squares) and July (triangles).
most fish have left the spawning grounds and remix with the rest of the adult population (the non-spawners) and so sampling in these months should be more representative of the overall female population. We found this to be true for only the July data (Figure 1). For ages 2 and 3 especially, the July data yielded greater proportions of mature females than either May or June. The July data were also more variable across years than those from the other months. May and June estimates of proportion mature varied in magnitude but followed similar time trends; the July pattern is different. We conclude that in the July data, problems in judging gonad status may be substantial, and the relative consistency of May and June values suggests population sampling was not seriously biased toward a non-reproducing subpopulation in May. We therefore decided to eliminate the July data from further analyses.

We also found that in a few of the years, average forklengths declined between May and June. Since fish do not shrink in this way, these occurrences must result from non-representative sampling of a highly clumped, heterogeneous fish stock. In order to moderate the sampling errors we averaged May and June data on maturity status in a given year, to make interpretation of the results more reliable. Therefore, in all further calculations and graphical representations, the maturity data as well as the length and weight data represent averages among May and June, with the months equally weighted.

**Growth rates**

Before growth rates were calculated, the data on forklength and round weight were assessed for normality and skewness for each year using the Kolmogorov-Smirnov test.
More than half of the years showed slight positive skewness. Therefore we used geometric means to represent central tendency for lengths and weights.

Growth rates were computed separately using forklengths and round weights as

\[ G = \frac{\ln L_2 - \ln L_1}{t_2 - t_1} \]

where \( G \) is the instantaneous growth rate, \( L_2 \) is the geometric mean forklength (mm) or round weight (g) at age \( t_2 \) and \( L_1 \) is the size at age \( t_1 \).

When the growth rates in ages 0-2, 2-3 and 3-4 were related with one another and with the proportion maturing, the \( x \) and \( y \) variables were always for the same cohort. That is, the proportion maturing at age 3 in spring 1985 was paired with the growth rate from 1982-1984 (0-2 years) for 2 year olds in 1984. Since we did not have any size data on 0+ or 1 year olds, the value of 5mm was chosen as the length at hatching for calculation of all growth rates (Craig 1987). Craig (1987) suggested that hatching yellow perch larvae range between 4 to 6mm and so we chose the middle of the range as the length at age 0 and used that value in the calculation of growth rates between 0 and 2 years. We then calculated average growth over the first 2 years of life (i.e. from 5mm to the mean of 2 year olds).

**Logistic regression**

We explored the hypothesis that the effect of condition on the probability of maturation varied with the size class of female yellow perch. A logistic regression of maturation (classified as 0=immature and 1=mature) on forklength (pooled across all years and ages
2-4 years) was used to classify yellow perch into three categories: 0-50%, 50-90% and >90% probability of maturing.

**Measurement of condition**

The traditional condition factor \((W/L^3)\) would not be size-independent if the weight-length regression does not have a weight intercept of zero (Jackson and Somers 1991). To eliminate this potential bias, our condition index was the residual in weight from a log-log weight-length regression. For each of the 3 size ranges associated with a level of maturity (e.g. 0-50% maturity range included fish 0 to 164 mm), the corresponding log (weights) were regressed on the log (forklengths) and the residual from the predicted weight was computed for each fish.

To identify and eliminate outliers in the weight-length regressions, boxplots of both the weight and length were drawn for the size ranges corresponding to the 3 maturity levels, and 2.5 times the IQR (inter-quartile range) was taken (Sokal and Rohlf 1995). For the 0-50% size range, out of 4083 data points, 1.05% lay outside this range and were classified as outliers. While for the 50-90% size range, 1.2% of 1904 data points were considered outliers. For the >90% size range, 2.7% of 2285 data points were removed as outliers. All outliers were eliminated before any statistical analyses on size, growth rates or condition.

The effect of condition on maturation was assessed by first estimating the mean deviation from the predicted weights for only the mature fish. Then, the mean
residual weight for mature fish was correlated with the proportion mature in the corresponding year to test whether, in years where there was a large proportion of fish reproducing, the mean condition of the mature fish was relatively high. This regression of log forklength against log weight and the correlation of residual weight for mature fish with the proportion mature in each year was performed separately for the 0-50% mature, 50-90% mature and >90% mature size groups.
RESULTS

Temporal variation in proportion mature

Temporal variations in the proportion of mature female yellow perch were not consistent across all ages (Figure 2). Variations in the proportion mature for ages 2 and 3 were correlated across years ($r=0.58$, $p=0.038$). Age 4 was less well correlated with both age 2 ($r=0.38$, $p=0.197$) and age 3 ($r=0.497$, $p=0.084$). The Durbin-Watson test showed no autocorrelation among the variable proportion mature for each age class across years.

The proportion mature for all ages was high in 1979 and was relatively low in 1983-1984. The age 4 fish recovered quickly and hovered around the 95% mark. The age 2 and 3 fish remained low after 1984, fluctuating between 0% and 10% (age 2) and 40% and 70% (age 3). Age 3 fish exhibited the largest interannual variation ranging from a high of 92% to a low of 42%. Age 4 maturity ranged from 97% to 60% and age 2 fish ranged from 0% to 18%.

Size and growth rates vs. proportion mature

The proportion mature was positively correlated with average forklength for all 3 age classes (Figure 3).

There was no statistically significant correlation between the growth rate in year 3 and the proportion that matured at the end of year 3, or for the growth rate in year 4 with the proportion that matured at the end of year 4 (Figure 4). Therefore, the rate of growth in
Figure 2. Interannual variation for the months of May and June (averaged) in the proportion of female yellow perch age 2 (open circles), age 3 (squares) and age 4 (triangles) classified as mature in Lake Erie. Age 2 fish are shown on the secondary axis.
Figure 3. Proportion of age 2 (a), age 3 (b), and age 4 (c) mature female yellow perch for years 1978-1990 as a function of forklength. The original observed values of the proportion mature are plotted. The numbers above the points are years. Equations are based on the arcsine square root transformation of the proportion mature.
Figure 4. Growth rates in the previous year versus the probability of being mature ($p_{\text{mat}}$). Growth rates in year 3 correlated against the probability of maturing at the end of year 3 using forklengths (a) and round weights (b). Growth rates in year 4 versus the probability of maturing at the end of year 4 using forklengths (c) and round weights (d). The numbers above the circles represent the year of maturation.
the previous year did not determine the proportion that would mature at the end of that growth period.

We expected according to typical growth models that high rates of growth in the early years would lead to growth rates reaching an asymptote sooner as energy is diverted from growth in length to growth of a gonad. Slower growth in the early years would lead to growth rates reaching an asymptote later (thus maturing later). This is because a slower growing fish would take longer to reach a critical length before maturation can occur.

There was a significant positive correlation between the growth rate in the first 2 years of life and the probability of maturation at the end of year 2 (Figure 5). The growth rate from age 0 to 2 was tested separately against the growth rates for the same cohort in year 3 and year 4 to see whether early growth dictated the growth rate (and hence maturation) in later years (Figure 6). We found yellow perch growth rates in their first 2 years tended to be negatively related with the growth rate in years 3 and 4 (Figure 6) although for year 4 it was non-significant.

**Linear regressions of forklength vs. weight derived from the logistic regression**

Three size ranges were determined using the logistic regression (Figure 7). Mature adult fish ranged in forklength from ~80mm to ~280mm. 50% of the fish reaching lengths of 164mm had matured while 90% of those 184mm in length had matured (Figure 7). The smallest size range encompassed fish whose forklengths ranged from 85mm (0% maturity) to 163mm (50% maturity). The intermediate size range included fish forklengths from 164mm (51%) to 183mm (90%). The largest size range included fish
\[ y = -356.258 + 224.279x \]
\[ r^2 = 0.60, \ p = 0.002 \]

Figure 5. Growth rates in length from ages 0 to 2 correlated with the probability \( (p_{ma}) \) of maturing at the end of year 2. The numbers above the circles represent the year of maturation.
Growth rate (age 0 to 2) vs. Growth rate (age 2 to 3) (a)

\[ y = 2.569 - 1.426x \]

\[ r^2 = 0.36, p = 0.039, n = 12 \]

Growth rate (age 0 to 2) vs. Growth rate (age 3 to 4) (b)

\[ y = 1.777 - 1.001x \]

\[ r^2 = 0.212, p = 0.15, n = 11 \]

Figure 6. Growth rates in length from ages 0 to 2 correlated with growth rates for the same cohort from ages 2 to 3 (a) and ages 3 to 4 (b).
Figure 7. Logistic regression of combined 2, 3, and 4 year old female yellow perch. Fish were classified as 0 (immature) or 1 (mature).
>183mm. Equations to predict round weight from forklength were derived for each maturation category (Figure 8).

**Correlation of condition (residual weight) with proportion mature**

For the smallest size range of adults, mean residual weight (hence fatness and condition) was weakly positively correlated with proportion mature, explaining approximately 25% of the interannual variation (Figure 9). Although there was a positive slope between the proportion mature and residual weight for the other two size ranges, residual weight explained only 8% and 10% of the variation in the proportion mature (Figure 9). Thus, the among-year variation in the proportion mature for a size group was only very weakly related to condition. However, the average deviations of reproducing fish were positive for 10/13 years for intermediate size fish and 11/13 years for the largest size range. In contrast, for the smallest size range, reproducing fish were heavier than average only 6 out of the 13 years. We found that for the smallest size range, the mature fish were approximately 5% larger than the average fish, while mature fish were 3.8% larger for the intermediate range and almost 6% greater for the largest size range of fish. Therefore overall, mature fish were heavier than average, but the among-year variation in condition was not strongly correlated with variation in the proportion maturing.
Figure 8. Fork length for various size ranges related to maturity status, as determined by the logistic regression. Log weights were regressed on log fork lengths for each level of maturity: (a) 0-50%, (b) 50-90%, and (c) >90%.
Figure 9. Mean deviations from predicted weight of only mature fish at 3 levels of maturity: 0-50% (triangles), 50-90% (circles) and >90% (stars) correlated with the proportion of females mature in that size range in the corresponding year. The actual proportions are plotted. Average residual weights for each maturity range are: low = 0.0012 +/- 0.0059 (SE); intermediate = 0.0077 +/- 0.0053; high = 0.019 +/- 0.0056.
DISCUSSION

Not all mature perch reproduce annually

We found that the 'actual' spawning stock size of yellow perch in Lake Erie is substantially smaller than what would be estimated based on the assumption that after first maturation, reproduction is annual. On average, over the 13 years of the study, 4% of 2-year old, 63% of 3-year old, and 92% of 4-year old females developed eggs in any given year. The proportion of mature adult female yellow perch in Lake Erie also varied greatly over this period. The ranges of variation were 20% (age 2), 50% (age 3) and 40% (age 4) respectively (Figure 2). Population fecundity may therefore be substantially less than that assumed. We would expect that such large changes in the proportion mature would contribute to the large observed fluctuations in year class strength (i.e. recruitment), characteristic of yellow perch in Lake Erie. The poor relationship between stock and recruitment for yellow perch may be partly explained by this variability.

Size affects the likelihood of maturation

In determining what may be causing the variation in the proportion mature, we asked whether size, growth rates or the condition of the fish is related to the probability of maturing. We found that, across years, the average length for a 2-year old fish was positively related to the proportion of the population maturing for the first time that year. Several earlier studies have reported that the probability of first maturation was positively related to the length of the fish (Myers et al. 1986; Simpson 1992; Berglund 1995; Whalen and Parrish 1999). Myers et al. (1986) suggested that a 'critical size' or energetic status is required to be reached before maturation can occur. They found that
male Atlantic salmon parr had a size threshold of 72 mm below which males never mature (Myers et al. 1986). Whalen and Parrish (1999) and Berglund (1995) both found that no parr <100 mm total length would mature. Note that the differences between 72 and 100 mm thresholds suggests that, if a threshold exists, it is population-specific. Our data suggests that female yellow perch would not begin to mature until reaching a size of at least 115 mm forklength. Myers et al. (1986) suggested that this critical length is required before sufficient energy stores are available for maturation and post-spawning and winter survival. Size may affect the potential to acquire food during a critical period in the year of maturation, and/or larger fish may already possess more energy than is necessary to meet the needs associated with sexual maturation (Simpson 1992; Berglund 1995). In Atlantic salmon parr, Simpson (1992) found that the %fat and forklength were strongly correlated. If a fish needs a certain level of fat to achieve maturation and fat and forklength are closely related, then there will be a size threshold associated with maturation.

Higher maturation rates of age 3 and 4 fish were also observed in years where average size was high. Individual fecundity is also positively related to size, and would therefore amplify the effects of the proportion mature on population fecundity. One factor that could result in year-to-year differences in forklengths and hence the proportion of mature female fish could be variation in the abundance or availability of an important food organism. Trippel and Harvey (1988) showed that white suckers that reproduced annually accumulated larger somatic weight and length gains than those fish that reproduced less frequently. They postulated that the less than annual maturation was due
to a resource-poor environment (Trippel and Harvey 1988). Tyler and Dunn (1976) suggested that female winter flounder adopted a strategy of maintaining body weight at the expense of oogenesis when food was in short supply, as was also postulated for haddock (Hislop et al. 1978). Poor habitat or food availability may explain the changes seen in the mean population lengths and the corresponding proportion of mature female fish observed in Lake Erie yellow perch over the time period studied here. Significant annual gains in length due to an increase in food availability would lead to a greater proportion of maturing females in the population of all ages.

Prior to the 1970's, high rates of nutrient loading caused rapid eutrophication causing a loss of large invertebrates and a reduction in the average size of benthic prey (Hayward and Margraf 1987). Although phosphorus inputs were reduced in the early 1970's, the prey resource base for Lake Erie yellow perch remained small-sized until about 1983 (Hayward and Margraf 1987). We observed that both the length of perch and the proportion mature declined from 1979 to 1984 for all age classes. Large fish were most affected by the effects of eutrophication in the western basin (Hayward and Margraf 1987). Large yellow perch (>175mm) in the western basin fed mainly on large-sized benthos (i.e. Hexagenia spp.) and on fish prior to 1970 (Hayward and Margraf 1987; Hayes and Taylor 1990). Lack of larger prey has been proposed by some researchers to impose an ontogenetic size limit (Hayward and Margraf 1987). As the number of prey fish (such as alewife, smelt and gizzard shad) declined, large adult yellow perch made a dietary switch from mainly fish and benthos to mostly benthos and zooplankton (Hayward and Margraf 1987; Hayes and Taylor 1990).
Reduction in the quality and/or abundance of food could have lead to the decline in the proportion of 2-year old fish maturing during early to mid-80's (Trippel 1995: Berglund 1995 (Atlantic salmon)). For Lake Erie perch, the smaller prey base observed in the early 80's would be well-suited for the gape size of smaller perch while it would be less suitable for larger fish who handle small prey items inefficiently (Hayes and Taylor 1990). Therefore the state of Lake Erie during 1978-1984 may have favoured younger and disadvantaged older yellow perch, due to the small average prey size. The prey resource base may have favoured the younger fish, but in fact, smaller fish also had to deal with feeding on lower total caloric prey items (such as oligochaetes and chironomids compared to feeding on items such as Hexagenia sp.), although the densities of these food items remained high (Hayward and Margraf 1987). As the system began its recovery after 1984, with the appearance of large-sized benthos and some of the forage fishes, the growth of yellow perch improved, and consequentially the proportion of females reproducing increased. Therefore, the observed qualitative and quantitative changes to the diet of yellow perch during 1978-1990 in response to changes in the degree of eutrophication in Lake Erie may have directed the temporal changes in mean fish population lengths and the fraction of maturing female yellow perch in the 80's and early 90's.

*Growth rates cannot predict maturation*

We found that the growth rate in the previous year did not determine the proportion that would mature at age 3 or age 4. For male Atlantic salmon parr, Thorpe (1986) found
growth rates in the preceding spring were positively correlated with the probability of gonadal recrudence in the autumn. However, once recrudence began, growth rates of maturing fish dropped to levels at or below the growth rates for non-maturing fish of similar age (Thorpe 1986). Rowe et al. (1991) found that specific monthly growth rates for maturing and non-maturing male Atlantic salmon parr did not differ at the earliest age of maturation and concluded no relationship between growth rates and maturation existed. However, on average, the maturing male parr were larger than the non-maturing parr (also true for perch here), thus indicating that the maturing parr experienced faster growth rates during the first year of life resulting in the larger initial length at the beginning of the second year of life. Myers et al. (1986) and Berglund (1995) also found no evidence that growth rates during the first of life were positively correlated with total proportion of male Atlantic salmon parr that matured within a year class. Therefore, we conclude that growth rate after first maturation has been reached is not a good predictor of subsequent reproduction.

However, we did find a strong correlation between the growth rate from age 0 to 2 and maturation at age 2. Therefore, if a cohort grows quickly in the first 2 years of life, the probability of maturation was high for the end of the second year since the individual fishes would have reached the ‘critical size’ faster. Faster mean growth rates have found to be positively related with early maturation in salmonids (Thorpe 1986). Specifically, it has been suggested that growth during a ‘critical time’ of the year is an important determinant of whether or not a fish is going to mature (Rowe et al. 1991). We found the growth rate from age 0 to 2 years old was negatively related to the growth rate from age 2...
to 3 and 3 to 4 years old. If a fish did not grow as quickly in the first 2 years of life and did not mature, our data suggest that it may make up in growth in later years. A later age at first reproduction might allow more energy to go into growth in the early years and the result is higher initial fecundity as well as increased ability to survive starvation and predation after a spawning event (Roff 1983; Trippel and Harvey 1988; Stearns 1992).

**Body condition has a relatively small effect on the probability of maturation**

The mean condition of mature females was positively related (although not significantly) to the proportion of mature female yellow perch only for the smallest size (and younger) range of fish: fish that would be maturing for the first time. We did not find a significant relationship between mean condition and the proportion mature for larger fish although slopes were still positive. However, we did find that the mature fish were on average 3.8% to 6% heavier than their non-maturing counterparts. Furthermore, our weight residuals are probably a conservative measure of energetic condition of a fish. It is well known that water content increases as fat levels fall, therefore dampening the relation between body weight and energy content (Chellappa et al. 1995). Thus, despite the lack of a strong relationship between condition and the probability of maturing, we cannot fully discount the effect of condition. Before a reliable assessment of the effects of condition can be conducted, direct calorimetry should be used to measure the true energetic status in mature female yellow perch. Many studies support the idea that higher fat levels are linked to the onset of maturation. Bohlin et al. (1994) specifically found that condition had a significant positive effect on the probability of maturing for male Atlantic salmon parr (Rowe et al. 1991: Simpson 1992). Rowe et al. (1991) found that
though both maturing and non-maturing fish increased fat levels in early spring, those fish that went on to mature had lipid levels that surpassed a minimum threshold level during a critical period in the annual cycle that would be able to fuel both gonad growth and survive winter (Simpson 1992). Individuals that maintained an immature state had failed to meet nutritional requirements necessary for gonadal maturation (Tyler and Dunn 1976: Hislop et al. 1978).

In summary, we have presented evidence that the proportion of mature female yellow perch in Lake Erie varies yearly and that the temporal variation is correlated only among fish ages 2 and 3. This variability may help to explain the poor relationship between stock and recruitment. Growth was the strongest correlate of the fraction of maturing females for all ages, thus fisheries managers could use the mean length at age in the autumn prior to the spawning period to estimate the fraction of females that will mature in the spring. Direct calorimetry measures of energetic condition should be investigated to enhance the precision of predictions based on size alone.
REFERENCES


Chapter 3:

Reassessing the stock in the stock-recruitment relationship: effects of interannual variations in the stock quality on the population fecundity and year class strength of Lake Erie yellow perch (*Perca flavescens*)
ABSTRACT

The assumption that the spawning stock biomass is directly proportional to population fecundity may not be valid because of changes in age or size distributions and the size-related differences in fecundity, as well changes in the proportion of female fish actually maturing. In a model we used known interannual variations in body size, age distribution, and the proportion mature for yellow perch in western Lake Erie to investigate the potential influence of natural variation in each of these parameters on population fecundity. Natural variation in these 3 aspects of stock quality are not powerful enough to explain occasional appearance of huge year classes but they are sufficiently powerful to account for most of the more typical interannual variation in YCS between the strong year classes. Of the 3 aspects of stock quality assessed, among-year variation in size at age, with associated changes in fecundity was the most powerful determinant of variation in fecundity. Despite the model's ability to generate several-fold changes in fecundity, it could not explain more than 13% of the measured variation in 0+ CPUE for the period 1978-1990. Random errors in measurement of stock abundance or quality, or unmeasured variations in egg quality and/or in the Lake Erie environment could potentially explain the low precision of the prediction.
INTRODUCTION

For percid populations, a standard stock-recruitment relationship cannot be detected statistically. Percid populations are characterized by sporadic strong year classes while the majority of years show relatively poor recruitment. Year class strength (YCS) in some populations such as *Perca fluviatilis* (Le Cren et al. 1977; Craig et al. 1979; Craig and Kipling 1983) and *Perca flavescens* (Henderson 1985; Norton 1997) is known to vary by 300 times between the strongest and weakest year classes. In general, recruitment appears to fluctuate independently of stock size except perhaps when stock sizes are exceptionally low (Koslow 1992).

For most species, recruitment is predicted from estimates of the size of the spawning stock, defined by the number or the biomass of sexually mature individuals. Traditional fisheries models of stock and recruitment (Ricker 1954; Beverton and Holt 1957) make the assumption that spawning stock size is proportional to the reproductive potential of the stock (i.e. the total potential egg production for a given stock biomass). The stock-recruitment relationship may be obscured by not including changes in reproductive parameters such as age and size distributions of the population, the energetic condition of females and, as introduced in the previous chapter, the proportion of sexually mature individuals within year classes.

In heavily exploited fisheries, the age distribution shifts markedly to younger ages. This change in age structure of the spawning stock may be important because younger age classes may have much lower fecundities than older ones. The reduced density
associated with exploitation may allow faster growth and enable fish to mature at a younger age. Reduced time to maturity may, in turn increase the survivorship to reproductive age. The earlier age at maturity has a powerful positive effect on population growth potential. These alterations to life histories help to compensate for the lower reproductive potential brought about by exploitative reductions in stock sizes (Trippel et al. 1997). However, depending on younger ages to uphold the population can be risky. Smaller, younger females may not be an adequate replacement for the older age classes normally found in unexploited populations.

A wealth of research suggests that egg quality, as well as egg number commonly varies with fish age. Maternal body size is correlated with both egg size and number for haddock, *Melanogrammus aeglefinus* (Hislop 1988), Atlantic cod, *Gadus morhua* (Kjesbu (1989) as cited in (Trippel et al. 1997)), herring, *Clupea harengus* (Hempel and Blaxter 1967), winter flounder, *Pseudopleuronectes americanus* (Buckley et al. 1991), and striped bass, *Morone saxatilis* (Zastrow et al. 1989). Larger eggs have been shown for Atlantic, Arcto-Norwegian, Icelandic cod, *Gadus morhua* (Knutsen and Tilseth 1985: Solemdal et al. 1992: Marteinsdottir and Steinarsson 1998), and *Fundulus heteroclitus* L. (Marteinsdottir and Able 1992) to produce larger larvae that have more vigorous activity, start feeding earlier, grow faster and ultimately have higher survival rates than progeny originating from smaller eggs (Chambers and Leggett 1996: Knutsen and Tilseth 1985: Hutchings 1991: Solemdal et al. 1992). It has also been demonstrated for Arcto-Norwegian cod (Solemdal et al. 1995). Atlantic cod (Kjesbu et al. 1996) and brown trout, *Salmo trutta* (Jonsson and Jonsson 1999) that there is lower hatching success from eggs
of first-time spawners than from second and third time spawners. Therefore, when a population is dominated by smaller fish that are maturing at an earlier age, the result is a reduction in the number of eggs spawned by the whole stock as well as a reduction in egg size with possibly reduced survivorship rates. Overall, the reproductive potential of the population is likely to be more significantly depressed than would be predicted from reductions in fecundity by themselves. However, increased survival to first reproduction may actually fully counteract the increase in fecundity resulting from another year in growth. Stearns (1992) points out that fitness is more sensitive to changes in life history traits for younger organisms than to equivalent changes in older organisms. Survival rates and fecundity were found to be important determinants of fitness for younger age classes.

The condition of the female spawner can also influence the quality of the resulting progeny (Trippel et al. 1997) and thereby the number of recruits, independent of the number of mature individuals. In a wide range of taxa, females that are found to be in good condition tend to produce larger and more eggs than lower condition females (Kjesbu 1994; Chambers and Waiwood 1996; Jonsson and Jonsson 1999). In some white sucker populations, female fish that were considered mature but were in weak energetic condition either produced very few small eggs or skipped a reproductive event altogether (Trippel and Harvey 1988). Positive correlations for Icelandic cod have been detected between female condition and larval feeding success and specific growth rates of larvae (Marteinsdottir and Steinarsson 1998). Such maternal effects are just beginning to be
explored by fisheries researchers. More research will be required before it is possible to assess the significance of maternal effects.

Another reproductive parameter closely related to the condition of the female fish that is overlooked in the calculation of the spawning stock biomass is the proportion of females of mature age that are actually reproducing in any one year. It is usually assumed that spawning occurs every year after a fish has reached first maturation. Recent work on northern fish species (e.g. Arctic charr and Atlantic salmon) and on a temperate fish (walleye) have shown that environmental stresses can inhibit reproduction, forcing mature females to skip spawning events (Dutil 1986: Jorgensen et al. 1997: Whalen and Parrish 1999). Henderson and Nepszy (1994) suggested that strong year class strength in walleye was probably a function of all potential female spawners contributing eggs because they had an energy surplus needed for the requirements of reproduction, whereas poor year classes occurred when a smaller fraction of potential females spawned because of poor energetic condition. Overall, the ‘actual’ annual spawning stock is another variable that should be considered by fisheries management, as it may account for significant variability in the reproductive potential of the spawning stock. Careful consideration of both the quantity and the quality of the eggs produced by a younger and smaller fish should be taken into account.

To assess the role of some of these aspects of stock quality in determining YCS (yearclass strength), a model was constructed to see how changes in the age and size distribution and proportion mature of female yellow perch (*Perca flavescens*) would
affect total egg production for the population and ultimately year class strength. The change in reproductive parameters included (i) observed magnitudes of change in the proportion mature as well as (ii) observed correlated changes in size and fecundity. and (iii) observed fluctuations in age distributions. To determine how the variation in fecundity generated by these changes in stock quality compared to the magnitude of natural variation in perch year class strength. we evaluated year class strength variation in 4 perch populations from the literature. In a more specific evaluation we ran the fecundity model using time series of measured changes in stock density. size distribution. and the proportion mature from western Lake Erie. and calculated how well we could hindcast measured variations in YCS over a 13 year period.
MATERIALS AND METHODS

Population fecundity model equation

Observed data on several life history traits (changes in the proportion mature, age and size distributions and related changes in fecundity) used in this model came from an earlier study (Chapter 1). Specifics from that study used in the model are included below.

The model equation used to calculate population fecundity was:

\[ F_p = \sum_{a=2}^{a=6} \bar{N}_a \times \bar{M}_a \times \bar{F}_a \]

where \( a = \text{age (2-6 years old)} \)

All variables were averaged over 13 years (1978-1990) in total.

\( \bar{F}_p = \text{average fecundity index of the population} \)

\( \bar{N}_a = \text{average CPUE of females age } a \)

\( \bar{M}_a = \text{average proportion mature at age } a \)

\( \bar{F}_a = \text{average fecundity at age } a \)

(1) Calculation of \( \bar{N}_a \):

Fish were collected from bottom-set, multi-panel gill nets in the Canadian waters of the west and west central basins during spring (1978-1990) (Norton 1997). Catch and effort data were combined for both basins for the spring gillnet sets for each year from 1978-1990 (Norton 1997).

Since not all age 2 fish are large enough to be recruited to the gear, the actual abundance of 2-year old fish in any year was calculated by extrapolation from the average CPUE of this cohort in the following year (i.e. age 3) assuming constant mortality with age.
The equation used was \( \ln N_{t+1} = \ln N_t - Z \) where \( N_{t+1} \) is the number at age \( t+1 \) and \( N_t \) is the number at age \( t \) (\( t \) is measured in years). In order to calculate the mortality rate, \( Z \), for a particular cohort, we graphed the natural logarithms of the CPUE of the various ages for a single cohort over a number of years. A line of best fit through these data will have a slope equal to the instantaneous mortality rate, \( Z \). We took the abundance at age 3 (the value of \( N_{t+1} \)) and the mortality rate (calculated separately for each cohort) to extrapolate backwards to find the age 2 abundance (\( N_t \)).

The average CPUE of females for each age was calculated as:

\[
\bar{N}_a = \frac{\text{CPUE}}{\text{Effort}} = \frac{\text{Catch}_{t,a}}{\text{Effort}_t}
\]

where \( t = \text{year} \) and \( a = \text{age (2-6 years old)} \).

(2) Calculation of \( \bar{M}_a \):

From empirical measurements based on gonad characteristics in May and June (Chapter 1), the proportions female yellow perch that had reproduced for each age and year were determined (Chapter 1. Figure 2).

To estimate the level of year to year variation in proportion mature for the model, the values for each year and age (Chapter 1. Figure 2) were arcsine-square root transformed. The means and standard deviations for all 13 years were calculated for each age. To generate the variation in fecundity associated with the 95% confidence limits of variation in proportion mature, the mean of the transformed proportion mature minus and plus 2 SD were backtransformed. Then the proportion mature in the model was varied over this range for each age class.
(3) Calculation of $\overline{F}_a$:

To find out how the average fecundity for an age class is related to the proportion mature ($p_{mat}$), we first predicted average forklength (flen) from an empirical relationship with the proportion mature (Chapter 1).

(3a) (i) Age 2: $\text{flen} = 0.769 \times \text{arcsine}(p_{mat})^{0.5} + 124.8$ $r^2 = 0.63$, $p = 0.001$
(ii) Age 3: $\text{flen} = 0.606 \times \text{arcsine}(p_{mat})^{0.5} + 138.07$ $r^2 = 0.35$, $p = 0.034$
(iii) Age 4: $\text{flen} = 1.229 \times \text{arcsine}(p_{mat})^{0.5} + 105.43$ $r^2 = 0.66$, $p = 0.0007$

To calculate the forklength from the proportion mature for ages 5 and 6, equation (3a)(iii) was used since there were insufficient data to develop equations individually for these ages.

Fecundity measurements based on egg counts of a known percentage of the ovary weight were taken in the month of April from a sample of aged 2, 3 and 4 year old adult female yellow perch with eggs. April is the month when they are the most fully developed before spawning. Fecundity for all other fish was then predicted from an empirical relationship with forklength.

$$F_i = a \times L^b \quad (\text{Figure 1a})$$

where $F$ is the fecundity of a female age ‘i’. $L$ is the average forklength of a female fish age ‘a’ and $a$ and $b$ are fitted constants.

(3b) $\log F_i = -3.7963 + 3.5011 \times \log L \quad r^2 = 0.79$, $p < 0.0001$ \quad (\text{Figure 1b})$

However, to use equation (3b) to predict the age-specific fecundity from the mean population length would underestimate fecundity because of the “fallacy of averages”
Figure 1. Fecundity versus fork length for individual fish aged 2, 3, and 4 that were fully developed in April (before the spawning period) in Lake Erie (a) and the log-log transformation of the fecundity and fork length relationship (b). The average fecundity and fork length for the population of age 2, 3 and 4 yellow perch in Lake Erie calculated for each year from 1978-1990 (c). The log-log transformation of the average population fecundity and fork lengths are shown in graph d.
(Templeton and Lawlor 1981). That is, the average of fecundities for a group of individuals of different lengths will not be the same as the fecundity of the average sized individual because the relation with length is nonlinear. That is, the lengths of fish in an age group are usually normally distributed about the mean length. If this is so, then a simple calculation of fecundity at the mean length will underestimate the mean fecundity of fish in the age group because the nonlinear relation of fecundity with size means that fish larger than the mean size contribute many more than half the eggs produced by the age group. To correct for this bias, we used the log-log relationship shown in Figure 1b to predict the fecundity of each fish of ages 2, 3 and 4 for each year from 1978-1990. We then averaged these fecundities and calculated the length for each age group for each year. A new log fecundity-log average forklength relationship was derived and used in the model (Figure 1c,d).

\[
\log F_a = -3.8392 + 3.5319 \times \log L \quad r^2 = 0.99, \quad p<0.0001 \quad \text{(Figure 1d)}
\]

where \(F\) is average fecundity of a female age \(a\). \(L\) is the average forklength of a female fish age \(a\). This calculation is the empirical equivalent of the analytical adjustment described by Pitcher and Macdonald (1973).

(4) Calculation of \(F_a\):

The index of average fecundity for the population \((F_p)\) using the model equation was then calculated using the average, lower 95% and upper 95% confidence limits of the proportion mature for each age. Because the variations in the proportion mature for the 3 age classes over our 13 years of data were positively correlated, our modelled deviations
in the proportion mature were applied in the same directions for all ages simultaneously. The ratio between fecundity indices generated from the upper and lower 95% confidence limits of proportion mature was used to measure how much variation in egg production could be generated by realistic changes in % maturity.

**Temporal variation in year class strength for percids**

Four studies showed the temporal distribution of percid year class strength is highly positively skewed (Table 1) (Craig et al. 1979; Henderson 1985; Norton 1997). We log transformed the individual year class strengths from a number of years from each study and found the 95% confidence limits. The log transformed mean with the 95% confidence limits were then backtransformed and the ratio of the upper and lower 95% confidence limits was calculated, which represents the magnitude of variation in year class strength that we can use to compare with those generated in the model runs.

**Sensitivity of YCS to reproductive parameters**

We constructed models of population fecundity based on observed age and size distributions and maturation rates for the period 1978-1990. Then we evaluated the contribution of each variable to the model’s ability to explain observed variation in YCS over this period observed. Recruitment ($R_{obs}$) are CPUE (catch per unit effort) of young-of-the-year yellow perch taken from mid- and bottom-water trawls in August and September, in the western basin of Lake Erie (Norton 1997). To calculate the expected recruitment ($R_{exp}$ = expected recruitment from the calculation of population fecundity) we used the model equation. The actual estimates of age-specific abundances, size-related
fecundities and the proportion mature collected from 1978-1990 were used in the equation. In order to assess how the level of information included in the calculation of \( R_{\text{exp}} \) was related to \( R_{\text{obs}} \), we started by holding all but one kind of data at its 13 year mean. For each subsequent test, more variables or different combinations were varied. When variables were held constant they were held at their average value calculated over the 13 years of data. We evaluated the relationship between observed recruitment and variation of +/- 2 SD in each of the following estimators of population recruitment.

(i) \( F_p = N \cdot \bar{M} \cdot \bar{F} \) (N varies)

(ii) \( F_p = N \cdot M \cdot \bar{F} \) (N and M vary)

(iii) \( F_p = N \cdot \bar{M} \cdot F \) (N and F vary)

(iv) \( F_p = N \cdot M \cdot F \) (all vary)
RESULTS

Population fecundity model equation

Altering the proportion mature +/- 2SD units changed total egg production by +/- 50% (Figure 2). The ratio between the high and low fecundities was 3.11 (Figure 2). The age 3 fish varied in fecundity by 25% and age 4 fish by 20%, in either direction of the mean proportion mature (Figure 3). The importance of age 3 fish reflects the fact that they exhibited the largest interannual variability in the proportion mature (Figure 4) even though the age 2 fish had by far the greatest abundances (Figure 5). When the proportion mature was low, ages 3 and 4 fish made up the majority of the total egg production (Figure 6). When the proportion mature was high, ages 4, 5 and 6 contributed the most to total population egg production (Figure 6).
The upper and lower values of the receptor index represent the upper and lower limits of the receptor's sensitivity. The numbers are the ratio between the mean and the standard deviation of the receptor's response to a stimulus. The arrows show the direction of the change in the receptor's response to a stimulus.

Figure 2. The squares represent the percentage increase or decrease in the mean proportion of eggs produced. The black squares represent the standard deviations around the mean proportion.
Figure 3. Percentage change in fecundity index of each age group at 95% confidence limits (mean + 2SD (squares)) and the mean - 2SD (circles) of level of maturity.
Figure 4. Range in the mean proportion mature for each age group used in the model, as defined by the 95% confidence limits for empirical observations on each age. The circles represent the proportion mature-2SD units and the squares represent the proportion mature+2SD units.
Figure 5. Abundance estimates averaged over the years from 1978-1990 for each age of yellow perch in Lake Erie.
Figure 6. The contribution of age 2 (solid), age 3 (vertical lines), age 4 (blank), age 5 (dots) and age 6 (diagonal lines) to the total population fecundity for different levels of the proportion mature for yellow perch in Lake Erie.
Literature values of year class strength for percids

All literature sources showed that the ratio of the strongest to the weakest year class strength in percids ranges from roughly 270 to 340 times. Our calculations show that the observed maximum/minimum ratio of perch YCS from the literature is equivalent to a ratio of 95% confidence limits of less than 4 (Table 1). Therefore, it appears that the range in variation in the observed proportion mature (3.11 X: Figure 2) might be nearly large enough to produce the range of variation represented by the 95% CL of interannual variation in YCS (Table 1).

Table 1. Literature values of variation in year class strength in percids and the range in variation in year class strength of the log transformed literature values.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Lake</th>
<th>Lake Size (km$^2$)</th>
<th>Fish Species</th>
<th># of years</th>
<th>Natural variation in YCS $^a$</th>
<th>Ratios of back-transformed 95% CL $^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Craig et al. 1979</td>
<td>Lake Windermere North basin</td>
<td>14 8 (total lake size)</td>
<td>European perch Perca fluviatilis L.</td>
<td>35</td>
<td>338</td>
<td>2.88</td>
</tr>
<tr>
<td>Craig et al. 1979</td>
<td>Lake Windermere South basin</td>
<td>14 8</td>
<td>European perch Perca fluviatilis</td>
<td>35</td>
<td>290</td>
<td>2.3</td>
</tr>
<tr>
<td>Henderson 1985</td>
<td>South Bay. Lake Huron</td>
<td>88</td>
<td>Yellow perch Perca flavescens</td>
<td>27</td>
<td>269</td>
<td>3.12</td>
</tr>
<tr>
<td>Norton 1997</td>
<td>Lake Erie</td>
<td>25090</td>
<td>Yellow perch Perca flavescens</td>
<td>17</td>
<td>276</td>
<td>3.6</td>
</tr>
</tbody>
</table>

$^a$ Ratio of highest to lowest year class strength observed

$^b$ On log transformed year class strength values, the mean +/- 95% confidence limits (CL) were backtransformed. The ratio between the backtransformed limits was calculated.

Relative importance of variability in reproductive parameters

One very strong observed year class strength (1980) was removed from the dataset before proceeding with any of the tests ($R_{\text{obs}}$ vs. $R_{\text{obs}}$). With the one strong year class strength value included, the ratio of the strongest to the weakest year class strength was 106 X. The strong year class was outside the range of the backtransformed 95% confidence interval and was therefore removed. The value deviated 3 SD's from the mean.
When we examined the relation of observed CPUE of 0+ fish to the predicted fecundity from the model, we found (Figure 7) the relationships were weak. With the inclusion of more information on reproductive parameters, the relationship between $R_{exp}$ and $R_{obs}$ improved, although not even the most complex model was statistically significant. Variations in fecundity with age and size contributed most strongly to the correlation (Figure 7c). Variation in percent of females maturing, and in the age distribution could account for almost none of the observed variation in YCS.
Variation in age distribution only ($F_r = N^*M(\text{avg})/F(\text{avg})$)

$$R_e = 8.196 - 1.3e^{-5}R_o,$$
$$r = 0.014$$

$R_e$ (Observed recruitment)

$R_o$ (Calculated total population egg production)

Age distribution and % mature vary ($F_r = N^*M(\text{avg})/F$)

$$R = 7.94 + 1.1e^{-5}R_o,$$
$$r = 0.012$$

$R_e$

$R_o$

Age distribution and fecundity vary ($F_r = N^*M(\text{avg})/F$)

$$R = 3.736 + 1.1e^{-5}R_o,$$
$$r = 0.097$$

$R_e$

$R_o$

(d) Age distribution % mature and fecundity vary among years ($F_r = N^*M^*$)

$$R = 3.322 + 3.6e^{-5}R_o,$$
$$r = 0.128$$

$R_e$

$R_o$

Figure 7. $R_e$ (expected recruitment is the calculated total population fecundity) versus $R_o$ (observed recruitment) of O+ yellow perch with increasing information included in the calculation of $R_e$ with each graph. The numbers above the points represents the year in which the new yearclass was born ($R_o$).
DISCUSSION

Influence of variations in the proportion mature on population fecundity

Our model was developed to assess how variation in the proportion mature could affect the egg production of a yellow perch population and to see if that variation is large enough to explain the substantial year to year fluctuations in recruitment. We found that natural variation in reproductive parameters was not powerful enough to explain the occasional appearance of very strong yearclasses, but was sufficient to produce most of the more typical interannual variation in YCS between strong yearclasses.

We found that the proportion of females reproducing was positively related to average forklength, which in turn was correlated with fecundity. Therefore, when we varied the mean proportion mature and the associated fecundity for each age class over a mean +/- 2SD range, to simulate the natural variability, we found that the total population egg production changed by +/- 55% from the mean. When the proportion mature was high, ages 3 and 4 fish contributed 39% and 35% respectively of the total population egg production. The age 2, 5 and 6 fish together made up only 26% of the total eggs produced. When maturation rates were at the low end of the range, fish were smaller than average and had low individual fecundity. Under these conditions, ages 4, 5 and 6 fish accounted for almost 75% the egg output of the population. This indicates, particularly in years when fish are smaller and thus a lower proportion of fish mature, there is an increased reliance on the contributions of larger/older fish to total population egg production.
Rijnsdorp et al. (1991) suggested that a reduction in the range of age groups contributing to the spawning population may reduce the chances for survival of the population. Lambert (1990) looked at the relationship between recruitment and the number of year classes present in the spawning population of Norwegian spring-spawning herring. He showed over a period of 19 years that better-than-average recruitment in herring was obtained when the spawning population was comprised of 3 or 4 age modes (modes represents the number of batches of spawning throughout the season and where each mode has more than one ageclass). There were no good year classes produced when the spawning population was unimodal. The age composition of the spawning population would be important if the age classes contributed unequally to reproduction (Marteinsdottir and Thorarinson 1998). The contribution of different qualities and quantities of eggs from a greater diversity of females (those of different ages. sizes and conditions) would enhance the chances of surviving to recruitment when the environment for eggs and larvae is limited and uncertain because this variation in eggs and resulting larvae would increase the probability of at least one offspring encountering favourable environmental conditions (Kjesbu et al. 1992). This could be an effective risk-spreading tactic which would help to ensure that at least a small proportion of the total larval population survives (Lambert 1990).

Sustainable yields for most fisheries occurs when females are allowed only once to reproduce before being caught (King 1995). Presently, for yellow perch in Lake Erie, we rely for the most part on small, inexperienced fish for reproduction. In fact, we found in years when the abundance of older aged fish (4, 5 and 6 year olds) made up a larger
percentage of the whole population. the recruitment was larger ($r^2 = 0.5$, $n=10$, $p=0.02$).
Although the age 2 and 3 year olds are very abundant. in our model the age 2 fishes contributed very little in respect to the total population fecundity. The age 3 fishes did however contribute the greatest percentage of the total population fecundity but the large variability in the proportion of age 3’s that matured. coupled with the fact that most of these fish are first-time spawners may help explain why strong year classes in this population have become less frequent and more sporadic. Hislop (1988) suggested that a weighting factor be applied to the different age classes in a fished stock on the assumption that the small eggs produced by small fish produce larvae that are less viable than the larger eggs of older fish. Many studies on a wide range of taxa have found positive relationships of both egg number and egg size with maternal length (Hempel and Blaxter 1967: Hislop 1988: Kjesbu 1989: Zastrow et al. 1989: Buckley et al. 1991: Trippel 1995: Trippel et al. 1997). For Lake Erie yellow perch. egg size was found to be correlated with fish length ($r^2 = 0.21$, $n=18$, $p=0.05$ in April: closest to the spawning season and $r^2 = 0.12$, $n=72$, $p=0.002$ in March) (T. Trivedi. unpublished). The result is an 11% (April data) and 7% (March data) increase in the fecundity from a mean length of a 3 year old fish (170mm) to a 5 year old fish (203mm). Although larger yellow perch made up a small proportion of the total spawning stock. the eggs from these larger and older fish could have enhanced survivability traits making them more likely to make it to recruitment. Larger eggs have been shown in turn to produce larger larvae which have higher rates of swimming activity. faster growth and higher survival rates (2X as high for Fundulus heteroclitus (L.) (Marteinsdottir and Able 1992)) than offspring resulting from smaller eggs and hence smaller fish (Knutsen and Tilseth 1985; Hutchings 1991:).
Solemdal et al. 1992). The larvae from those larger Fundulus heteroclitus (L.) eggs survived without food two times longer than those larvae from the smaller eggs and the size differences at hatching were still maintained after 42 days of growth (Marteinsdottir and Able 1992). Zastrow et al. (1989) found in striped bass that eggs reared by age 4 to 5 year olds had a 21% lower hatching success than eggs from fish aged 7-15. The increased quality of the eggs laid by older fish is not recognized in our model. Quantitative assessments of the relationship between perch egg size and aspects of fitness such as growth and survival rates should be undertaken to allow us to calculate more precisely the costs of removing older age classes.

To assess how much the variability in the proportion mature contributes to the variability in egg production and hence year class strength of percids, we compared our model results with the observed magnitude of variation in year class strength recorded in the literature. Percid populations are known to vary up to 400X between strong and weak year classes (Craig et al. 1979: Henderson 1985: Norton 1997), with much of that range produced by a few very large year classes that can be considered as outliers. Ranges this high are common for most percids and these few very large year classes produce highly positively skewed distributions.

Since most of the values of year class strength lie within the 95% confidence limits, we wanted to determine whether the variations in the proportion mature could explain that much of the variability. In nature, we found that the observed year class strength within the back-transformed 95% CI ranged between 2.88X and 3.6X. Our modelling showed
that the most extreme variation in proportion mature, including associated changes in female size and fecundity could produce year classes spanning over a 3.11X range. Variation in the proportion maturing, then, could explain a large proportion of the observed variation in recruitment between the occasional outlier year classes. However, these unusually large year classes must arise primarily from changes in egg quality or in the environment, rather than fluctuations in stock quality.

Variations in reproductive parameters could not predict observed YCS in nature

We used a time series of measured changes in stock density, size distribution, and the proportion of females maturing to determine how well we could hindcast measured variations in YCS over a 13-year period in western Lake Erie. As more information was entered into the model, the relationship between the observed and expected recruitment improved, but even with year-specific values of proportion maturity, age distributions, and size distributions, the model could only account for 13% of the observed variation in YCS. The contribution of the proportion mature parameter was small, explaining only 3.8% of the variability. Size-related fecundity explained more variance in YCS than any other single parameter. The low explained variance of the model contrasts with the findings of Marteinsdottir and Thorarinsson (1998) who explained 31% of variation in recruitment of Icelandic cod by including information on the age composition with stock sizes.
Reasons for lack of predictability of YCS

Our model of total population fecundity might be improved by adding a condition factor component (Trippel and Harvey 1988; Marshall et al. 1998). The energetic condition of females in the spawning stock varies year to year, presumably due to changes in food supply and other environmental factors (Henderson and Nepszy 1994; Trippel et al. 1997; Marshall et al. 1998). Both Chambers and Waiwood (1996) and Marteinsdottir and Steinarsson (1998) found positive relationships between egg size and Fulton's condition factor for females. Marshall et al. (1998) found in cod that the rate of population change was positively correlated with hepatosomatic index. They suggested that both age-specific abundance and condition of the females acting in combination would reduce total population egg production. Although egg size is related to female size in perch, it is unknown whether egg size varies further with female energetic condition. Positive relationships of egg size with female size would act to further amplify the variability in population fecundity such that spawning stocks made up of large fish will produce a greater number of larger eggs than those with smaller average female size.

Despite the fact that the magnitude of possible variations in the proportion mature was large enough to explain much of the observed variation in YCS, the timing was apparently not coordinated with YCS variation in the field so that the model could not effectively predict observed YCS. Typical and inevitable sampling errors in the measurement of stock and recruits may severely limit the precision of model predictions. One possible sampling error might occur when a management unit (there are 4 in Lake Erie) assumes a single, self-sustaining population (Frank 1997). In fact, the management
stock may contain more than one unit stock usually because of the large spatial scale of the management unit (Frank 1997). Aalto and Newsome (1993) found that yellow perch in Lochaber Lake in Nova Scotia displayed a demic structure at spatial scales ranging from 0.5 to 5 kilometers and that these demes exhibited independent population dynamics. In addition, recent work on the genetics of yellow perch stocks in Lake Erie has shown that during the post-spawning season, the western basin L. Erie yellow perch populations are influenced by subsequent recolonization (GLFC 1998). More work on stock identification on yellow perch in Lake Erie is still ongoing. Therefore, errors in the estimates of recruitment may occur due to emigration or immigration from and into the management unit stock. However, our dataset was characterized by substantial numbers of net sets, and it is unlikely that substantially more precise estimates of CPUE for adults and YOY would be logistically feasible. Another unaccounted-for source of error in stock-recruitment relationships is the intervention of unmodelled sources of mortality between the time of oviposition in May and the time YCS is assessed in the fall. Because the CPUE for YOY is not strongly related to the CPUE of 1± or 2±, then our use of YOY as our measurement of YCS is probably the best measure of YCS since these YOY fish would have experienced the least amount of mortality between the egg stage in April and before sampling took place in late summer. In addition, our model assumed constant mortality between ages 2 and 3 which might be a potential reason why our model could not explain the observed variation in YCS. If age 2 mortality was high and variable, this is potentially where the unexplained variance in YCS comes from since high mortality before age 3 would mean that the age 3, 4 and 5 year old fish who contribute the most number of eggs in good and bad years would be severely reduced.
In summary, errors in the measurement of both the adult stock size and recruitment indices and our failure to consider variations in egg quality and female condition undoubtedly obscured much of the explanatory power of our model. The $r^2$ of 13% is likely a substantial underestimate of the true contribution of stock quality to the variation in YCS.
REFERENCES


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Conclusions
This thesis is a re-evaluation of the effects of various environmental factors on the YCS of percids and the stock-recruitment relationship and its associated assumptions. In the first chapter we found that variability in YCS in percids generally could not be consistently and significantly related to any single environmental factor. In the second chapter we found evidence that yellow perch populations in Lake Erie are spawning intermittently. In the third chapter we found that the variability in the proportion of mature female yellow perch at age could explain most of the interannual variation in YCS but could not explain the occasional very strong year classes. In addition, the interannual variation in various life history parameters of the spawning stock could not accurately predict the observed recruitment found in nature. Directions for future work on yellow perch populations and generally on fish populations are discussed below.

**Directions for future research**

**Environmental variables**

The findings uncovered in this thesis suggest several avenues of research. First of all, research into the effects of environmental factors on YCS needs to take several new approaches. The difficulties in assessing any abiotic or biotic effects on YCS came mostly from the inaccurate or lack of reporting of statistics. This was greatly noticed especially when trying to do a meta-analysis. In many cases, r-values were not listed, nor were p-values or samples sizes (especially when they removed outliers without justifying why they removed them). All statistical reporting should include the test value, sample size used and the significance value, all of which are important if one wants to compare studies. Use of a meta-analysis to test similar hypotheses among a number of studies is a
powerful statistical tool that has recently gotten attention in fisheries research. However, another problem that exists in combining studies is that not only studies testing a similar hypothesis are required but how the hypothesis was tested needs to be similar. That is, the variables measured should be similar. Through meta-analytic techniques, temperature was found to be positively related to YCS however it did not explain most of the variation in YCS and furthermore, this meta-analysis combined various types of percids. It was also found that competition between white and yellow perch does not exist in Lake Erie and further research on this need not be done. As for wind, very few studies exist and its effect cannot be conclusively determined. The various ways of testing for predation effects by walleye on yellow perch has also made it difficult to conclude anything. Overall, a new approach to research in general should be that a robust method be developed to test a hypothesis and that method be carried out over a number of lakes inorder to assess whether a variables effect is an overall phenomenon or is it a lake-specific effect. Thus, judgements about a variable’s effect than can be more clearly evaluated in the management of a particular fish species.

Stock-recruitment relationships

The notion that spawning stock size is related to recruitment should be reconsidered. Work on improving the relationship may hold the key to accurately predicting recruitment and thus be able to set fishing quotas accordingly. Research into the variation in life history parameters, especially those associated with the adult female could give us further insight into exploited fish population dynamics. Ideally, an extensive model that incorporates the yearly variation of various life history parameters
of the spawning stock and environmental factors affecting early larval stages is needed to accurately predict YCS. Energetic condition for the adult female yellow perch derived from direct measurements of energy and its effect on the number of eggs and the condition of the resulting eggs and larvae are possible missing links in explaining the variation in YCS of perch.

Additionally, tagging experiments (perhaps on smaller lake systems) would allow one to follow fish throughout several years to observe any skipping of reproductive events.
Appendix
APPENDIX 1  Meta-analysis on temperature studies

Ho: Temperature is not positively correlated with YCS of percids
H1: Temperature is positively correlated with YCS of percids

\[
\ln P
\]

\[
r = 0.68 \quad n=11 \quad p=0.02 \quad -3.912023
\]

\[
r = 0.80 \quad n=9 \quad p=0.025 \quad -3.6888795
\]

\[
r = 0.63 \quad n=10 \quad p=0.05 \quad -2.9957323
\]

\[
r = 0.48 \quad n=8 \quad p=0.20 \quad -1.69094379
\]

\[
r = 0.82 \quad n=7 \quad p=0.05 \quad -2.9957323
\]

\[
\text{Total } -15.283311
\]

\[-2\sum \ln P = -2(-15.283311) = 30.566622\]

\[2k=2(5)=10\]

so \(x^2_{0.05[10]}=18.307\) or \(x^2_{0.001[10]}=29.588\)

Therefore, since our \(-2\sum \ln P\) is larger than \(x^2_{0.001[10]}\), we then reject the null and accept that there is a positive correlation between temperature and YCS.

We then check for the homogeneity of the correlation coefficients

Ho: \(p_0=p_1=p_2=p_3\ldots\)
H1: \(p_0\neq p_1\neq p_2\neq p_3\ldots\)

<table>
<thead>
<tr>
<th>(i)</th>
<th>(r_i)</th>
<th>(z_i)</th>
<th>(z_i^2)</th>
<th>(n_i)</th>
<th>(n_i3)</th>
<th>(z_i(n_i3))</th>
<th>(n_i3z_i^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.68</td>
<td>0.5915</td>
<td>0.3499</td>
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<td>8</td>
<td>4.732</td>
<td>2.79898</td>
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<tr>
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<tr>
<td>4</td>
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<td>0.4462</td>
<td>0.1991</td>
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<td>2.231</td>
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<tr>
<td>Total</td>
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<td></td>
<td></td>
<td>30</td>
<td>17.5541</td>
<td>10.4432</td>
<td></td>
</tr>
</tbody>
</table>

To calculate \(z_w = (n_i3)z_i = 17.5541 = 0.5851367\). where \(r_w = 0.5263\)

\[-\frac{30}{n_i3} = 0.5851367\]

\[
x^2_p = \frac{\sum n_i3(z_i - r_w)^2}{(1-(r_i - r_w))}
\]

\[
= \frac{11(0.68-0.5263)^2 + 9(0.8-0.5263)^2 + 10(0.63-0.5263)^2 + 8(0.48-0.5263)^2}{[1-(0.68)(0.5263)]^2 [1-(0.8)(0.5263)]^2 [1-(0.63)(0.5263)]^2 [1-(0.48)(0.5263)]^2}
\]

\[
+ \frac{7(0.82-0.5263)^2}{[1-(0.82)(0.5263)]^2}
\]

\[
= 0.6302509 + 2.011384 + 0.2406824 + 0.0307025 + 1.8687269
\]
Therefore, our calculated value of 4.78 is less than \( \chi^2_{0.05|4} = 9.488 \), therefore we accept the null that the correlation coefficients are homogeneous, and the common correlation coefficient is 0.53 (\( r_w \)).
APPENDIX 2 Meta-analysis on competition studies

Ho: no negative relationship between growth of yellow perch vs. abundance of white perch
H1: there is a negative relationship between growth of yellow perch vs. abundance of white perch

<table>
<thead>
<tr>
<th>r</th>
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<th>p</th>
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</tr>
<tr>
<td>0.27</td>
<td>19</td>
<td>0.72</td>
<td>-0.3285041</td>
</tr>
<tr>
<td>-0.17</td>
<td>19</td>
<td>0.51</td>
<td>-0.6733446</td>
</tr>
<tr>
<td>-0.19</td>
<td>18</td>
<td>0.54</td>
<td>-0.6161861</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>r</th>
<th>n</th>
<th>p</th>
<th>ln P</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.11</td>
<td>14</td>
<td>0.43</td>
<td>-0.8439701 YOY yp vs. adult wp</td>
</tr>
<tr>
<td>0.34</td>
<td>5</td>
<td>0.94</td>
<td>-0.0618754 YOY yp vs. YOY wp</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
</tr>
</tbody>
</table>

-2ΣlnP= -2(-3.0019161)= 6.0038322
2k=2(6)=12 so χ²[0.05][12]=21.026

Therefore, since our -2ΣlnP is smaller than χ²[0.05][12], we then accept the null that there is no negative relationship between growth of yellow perch and abundance of white perch.

We then check for the homogeneity of the correlation coefficients
Ho: p₁=p₂=p₃=...=pₙ
H1: p₁≠p₂≠p₃≠...

<table>
<thead>
<tr>
<th>i</th>
<th>rᵢ</th>
<th>zᵢ</th>
<th>zᵢ²</th>
<th>nᵢ</th>
<th>(nᵢ-3)zᵢ</th>
<th>(nᵢ-3)zᵢ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.22</td>
<td>0.2237</td>
<td>0.0500417</td>
<td>19</td>
<td>16</td>
<td>3.5792</td>
</tr>
<tr>
<td>2</td>
<td>0.27</td>
<td>0.2769</td>
<td>0.0766737</td>
<td>19</td>
<td>16</td>
<td>4.4304</td>
</tr>
<tr>
<td>3</td>
<td>-0.17</td>
<td>0.1717</td>
<td>0.0294809</td>
<td>19</td>
<td>16</td>
<td>2.7472</td>
</tr>
<tr>
<td>4</td>
<td>-0.19</td>
<td>0.1923</td>
<td>0.0369793</td>
<td>18</td>
<td>15</td>
<td>2.8845</td>
</tr>
<tr>
<td>5</td>
<td>0.11</td>
<td>0.1104</td>
<td>0.0121882</td>
<td>14</td>
<td>11</td>
<td>1.2144</td>
</tr>
<tr>
<td>6</td>
<td>0.34</td>
<td>0.3541</td>
<td>0.1253868</td>
<td>15</td>
<td>12</td>
<td>4.2492</td>
</tr>
<tr>
<td>Total</td>
<td>86</td>
<td>19.1477</td>
<td>4.6925421</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

To calculate zₘ = (nᵢ-3)zᵢ / (nᵢ-3) = 19.1477 / 86 = 0.2226477, where rₘ = 0.2184

χ²_p = ∑ (nᵢ-3)zᵢ² / (1-(rᵢ-rₘ))²

= 19(0.22-0.2184)² + 19(0.27-0.2184)² + 19(-0.17-0.2184)² + 18(-0.19-0.2184)² + 14(0.11-0.2184)² + 15(0.34-0.2184)²

[1-(0.22)(0.2184)]² [1-(0.27)(0.2184)]² [1-(-0.17)(0.2184)]² [1-(-0.19)(0.2184)]² [1-(0.11)(0.2184)]² [1-(0.34)(0.2184)]²

= 4.6925421
\[ V = k - 1 \]

\[ \chi^2_{[0.05][5]} = 11.070 \]

\[ v = k - 1 \]

\[ = 6 - 1 \]

\[ = 5 \]

Therefore, our calculated value of 6.10 is less than \( \chi^2_{[0.05][5]} = 11.070 \). Therefore we accept the null hypothesis that the correlation coefficients are homogeneous.
APPENDIX 3 Meta-analysis on competition studies-Version 2 (Only studies using adult fish)

Ho: no negative relationship between growth of yellow perch vs. abundance of white perch
H₁: there is a negative relationship between growth of yellow perch vs. abundance of white perch

<table>
<thead>
<tr>
<th>r</th>
<th>p</th>
<th>n</th>
<th>lnP</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.2</td>
<td>0.62</td>
<td>19</td>
<td>0.4780358</td>
</tr>
<tr>
<td>0.27</td>
<td>0.72</td>
<td>19</td>
<td>0.3285041</td>
</tr>
<tr>
<td>-0.17</td>
<td>0.51</td>
<td>19</td>
<td>0.6733446</td>
</tr>
<tr>
<td>-0.19</td>
<td>0.54</td>
<td>18</td>
<td>0.6161861</td>
</tr>
</tbody>
</table>

\[-2ΣlnP = -2(-2.0960706) = 4.1921412\]

\[2k=2(4)=8\] so \[x^2_{0.05||8|} = 15.507\]

Therefore, since our \([-2ΣlnP]\) is smaller than \(x^2_{0.05||8}\), we then accept the null that there is no negative relationship between growth of yellow perch and abundance of white perch.

We then check for the homogeneity of the correlation coefficients

Ho: \(p_0 = p_1 = p_2 = p_n\)
H₁: \(p_0 ≠ p_1 ≠ p_2 ≠ p_n\)

\[
\begin{array}{cccccccc}
\hline
i & r_i & z_i & z_i^2 & n_i & n_i - 3 & (n_i - 3)z_i & (n_i - 3)z_i^2 \\
\hline
1 & 0.22 & 0.2237 & 0.0500417 & 19 & 16 & 3.5792 & 0.8006672 \\
2 & 0.27 & 0.2769 & 0.0766737 & 19 & 16 & 4.4304 & 1.2267792 \\
3 & -0.17 & 0.1717 & 0.0294809 & 19 & 16 & 2.7472 & 0.4716944 \\
4 & -0.19 & 0.1923 & 0.0369793 & 18 & 15 & 2.8845 & 0.5546895 \\
\hline
\text{Total} & & & 63 & 13.6413 & 3.0538303 & \\
\hline
\end{array}
\]

To calculate \(z_\text{w} = \frac{(n_i - 3)z_i}{n_i - 3} = 0.2165286\), where \(r_w = 0.2127\)

\[
\chi^2_p = \frac{\sum (n_i)(r_i - r_w)^2}{(1-(r_i - r_w))^2} = 0.0011144 + 0.0702158 + 2.5918969 + 2.6966478
\]
\[ = 5.3598749 \]

\[ \nu = k-1 \quad x^2_{0.05|3} = 7.815 \]
\[ = 4 - 1 \]
\[ = 3 \]

Therefore, our calculated value of 5.36 is less than \( x^2_{0.05|3} = 7.815 \). Therefore we accept the null that the correlation coefficients are homogeneous.