Use of otolith microstructure to examine growth of young-of-year yellow perch (Perca flavescens): Linking diet to growth.

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USE OF OTOLITH MICROSTRUCTURE TO EXAMINE GROWTH OF YOUNG-OF-YEAR YELLOW PERCH (PERCA FLAVESCENS): LINKING DIET TO GROWTH

Alec Dale

A Thesis Submitted to the Faculty of Graduate Studies and Research Through the Department of Biological Sciences In Partial Fulfilment of the Requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada
2000
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ABSTRACT

Recent increases in aquatic macrophyte distribution and abundance in Lake St. Clair, Ontario have the potential to influence growth of important fishery species such as yellow perch (Perca flavescens). Laboratory-based research was first conducted to validate the assumptions of daily otolith increment formation and constant proportionality of the otolith-somatic growth relationship of juvenile yellow perch under changing rations. Otolith analysis was then coupled with diet and prey community analysis to determine if growth or diet of yellow perch differed between vegetated and non-vegetated sites in Lake St. Clair. Increment formation was daily in otoliths of juvenile yellow perch. Mean increase in fork length estimated from otolith increments was not significantly different from observed increase in fork length for all groups. There appeared to be a 1-2 d time lag between change in ration and change in increment formation; however, changes in increment formation were not statistically detectable until 5-10 d after a ration switch. In Lake St. Clair, vegetated sites generally had higher densities of chironomids, amphipods, ephemeropterans, and trichopterans, while non-vegetated sites had higher densities of oligochaetes and nematodes and Hexagenia mayflies. Discriminant function analysis successfully discriminated between vegetated and non-vegetated sites based on the invertebrate prey community. Diet of juvenile yellow perch reflected the available prey community and fish from both habitats fed predominantly on zooplankton during early July, but switched to a benthic invertebrate dominated diet by late August. Fish in non-vegetated sites continued to feed on zooplankton to a greater extent than fish in vegetated habitats. Mean size of fish was similar among the non-vegetated sites and one vegetated site. Fish from the two most vegetated sites were smaller than fish from non-vegetated sites on all sample dates, although not always significantly smaller. Growth rates, standardised to fish size, were not significantly different
among all sites during the first two sample dates. However, fish from the two vegetated sites had significantly lower growth rates than other sites during the last two sample dates. Differences in size and growth were most likely related to hatch date of juvenile yellow perch during 1998, and not habitat type.
DEDICATION

One fish, two fish, red fish, blue fish.
Black fish, blue fish, old fish, new fish.
This one has a little star. This one has a little car.
Say! What a lot of fish there are.

© 1960 Theodor Seuss Geisel

I have been interested and intrigued by fish and their lives since before I was old enough to read this passage by the esteemed unnatural historian, Dr. Seuss. This thesis is dedicated to the three most important people in my life. First, I want to dedicate this to my parents who, in every possible way, have supported and encouraged all of my interests. Second, when my motivation was at its lowest, my soul-mate Angela was able to provide me with valuable perspective by reminding me of the “big picture”, and those early days of innocent intrigue and wonder at the natural world around us.

Eventually, all things merge into one, and a river runs through it. The river was cut by the world’s great flood and runs over rocks from the basement of time. On some of the rocks are timeless raindrops. Under the rocks are the words, and some of the words are theirs. I am haunted by waters.

© 1976, Norman Maclean
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CHAPTER 1: General Introduction

ECOLOGY OF SHALLOW LAKES

The functioning of shallow lakes throughout the world is often very different from the more 'traditional', deep lakes described in limnology texts. Shallow lakes generally experience thorough mixing of the entire water column (polymictic), and their shallow nature translates to a large portion of the sediment surface area being suitable for colonisation by aquatic macrophytes (Scheffer, 1998). Deeper lakes, in contrast, are often highly stratified, and generally have only a narrow littoral zone that is suitable for aquatic plant colonisation. In addition, the close relationship to the sediment leads to increased internal abiotic and biotic interactions making shallow lakes more dynamic than deep lakes. Many shallow lakes can be viewed as occurring in either of two alternating states of equilibrium (Timms and Moss, 1984; Moss, 1990; Scheffer et al., 1993; Moss et al., 1996; Scheffer, 1998). These two equilibria, maintained by internal stabilising mechanisms, are a macrophyte dominated, clear water state and a phytoplankton dominated, turbid water state. Refer to Scheffer (1998) for an excellent review of both these mechanisms and the general ecology of shallow lakes.

Light limitation is often the main factor limiting macrophyte colonisation and stabilising the turbid state in shallow lakes. For 90 lakes throughout the world, Chambers and Kalff (1985) found a highly significant positive correlation between Secchi depth and the maximum depth (to 12-13 m) of aquatic angiosperm colonisation. The change from a naturally vegetated, clear water state to a more phytoplankton dominated, turbid state is often mediated by increased nutrient loads to the system (Scheffer, 1998). Moss (1990) points out that the catchment areas of many shallow lakes often contain high anthropogenic inputs of nutrients via intense agricultural, industrial, or municipal activities. As well, many shallow lakes have an available reservoir of high internal nutrient loads present in the sediment.
(Marsden, 1989). Both of these sources can combine to produce highly eutrophic systems. World wide, this increased eutrophication is associated with increased phytoplankton production, which acts to decrease light penetration in the water column (Wetzel, 1975). Scheffer (1998) notes that macrophytes will disappear once the increasing production of phytoplankton produces a critical level of turbidity. Once the stabilising structure of macrophyte root systems disappear, turbidity increases due to resuspension of sediments by waves or bioturbation by macroinvertebrates or fish, further reducing the colonisation potential of macrophytes and stabilising the lake in the turbid state.

For the lake to shift back to its previously clear, macrophyte-dominated state the same critical level of turbidity must be overcome. However, the presence of macrophytes themselves can lead to decreased turbidity and provide a positive feedback for additional macrophyte growth (Scheffer, 1998). Increasing aquatic macrophytes can reduce turbidity in several ways. First, phytoplankton populations and associated turbidity can be reduced via competition for nutrients with macrophytes. Macrophytes are often able to utilise and store available nutrients more efficiently than phytoplankton (Wetzel, 1975; Rørslett et al., 1986; Mjelde and Faafeng, 1997). Second, some macrophytes have an allelopathic affect on phytoplankton stocks (Brammer, 1979; Wium-Andersen et al., 1982), again resulting in decreased abundance and turbidity. Third, increases in macrophytes are known to enhance piscivorous-based fish communities, as opposed to planktivorous communities (Grimm, 1989; Grimm and Backx, 1990; Van Donk and Gulati, 1995). This can lead to a predation-related reduction in the planktivorous fish community, allowing larger bodied zooplankton to more effectively graze phytoplankton. In fact, manipulations or reductions of planktivorous fish populations, either directly or by enhancing piscivorous species, are often utilised to decrease lake turbidity (Grimm and Backx, 1990; Brönmark & Weisner, 1992;
Lauridsen, et al., 1994; Schriver et al., 1995). Finally the physical structure of macrophytes in the water column and their extensive root systems can effectively reduce turbidity by stabilising sediments that would have previously been resuspended by wave action (Engle, 1995; Scheffer, 1998). In general, the importance of these stabilising factors in maintaining a particular equilibrium will vary from lake to lake. However, these factors are significant buffers that act to maintain a particular lake in whatever equilibrium state it happens to be in, often over a wide range of trophic states and latitude (Mjelde and Faafeng, 1997).

The general trend in management of lake environments in recent years has been to try to decrease nutrient loading in the hope that this will reverse the trend of eutrophication brought on by previous anthropogenic nutrient loadings. However, a reduction in nutrient loads, in itself, is often not enough to overcome the critical turbidity needed to return a lake to a macrophyte dominated state (Scheffer et al., 1993; Scheffer, 1998). In these cases, a reduction in nutrient loads coupled with a perturbation to the system is often required to reduce turbidity to a critical level and trigger a switch to a more desirable macrophyte dominated state (Moss, 1990; Scheffer et al., 1993; Scheffer, 1998). Such a shift from a phytoplankton dominated, turbid state to a macrophyte dominated, clear state can obviously have far reaching implications throughout the system.

IMPACTS OF VEGETATION IN SHALLOW LAKES

Increases in aquatic macrophytes can have profound influences on the abiotic and biotic environment in shallow lakes. Extensive cover of floating or emergent plants can provide shelter from the wind, reduce turbulence and aeration, restrict mixing, and promote thermal stratification (Engle, 1985). Higher water temperatures, lower pH, and lower
dissolved oxygen have all been associated with increased macrophyte cover (Frodge et al., 1990).

Changes to macrophytes and concomitant changes to the numerous epiphytic and benthic invertebrate fauna associated with aquatic macrophytes can in turn alter prey availability and abundance for various fish species. For example, abundance and diversity of epiphytic invertebrate species have been correlated with area, biomass (Cyr and Downing, 1988; Lalonde and Downing, 1992), and species composition (Dvorak and Best, 1982; Keast, 1984; Dionne et al., 1990; Dionne and Folt, 1991) of aquatic macrophytes. As well, Rasmussen (1988) found that increased abundance of submerged macrophytes negatively influenced abundance of benthic mayflies (Hexagenia spp.), and noted that mayflies were important prey items for many fish species, including yellow perch (Perca flavescens).

In general, there is an initial increase in fish foraging efficiency and growth correlated with increased aquatic macrophyte abundance, biomass (Devries et al., 1989; Gotceitas and Colgan, 1990), and structural complexity (Diehl, 1988; Dionne and Folt, 1991; Chick and McIvor, 1994). However, above a certain degree of structural complexity, foraging efficiency and growth of fish is often reduced with maximum foraging and growth seen at intermediate levels of macrophyte abundance (Diggins et al., 1979; Dionne and Folt, 1991; Trebitz and Nibbelink, 1996). Olson et al. (1998) were able to experimentally increase growth rates of bluegill and largemouth bass of certain age classes by removing macrophytes from approximately 20% of the littoral zone of four Wisconsin lakes. Finally, increased macrophyte cover and complexity have been shown to offer refuges against piscivory for many small fish species or young-of-the-year (YOY) of larger fish species (Rozas and Odum, 1988; Savino and Stein, 1989; Gotceitas and Colgan, 1990).
STUDY SYSTEM

Lake St. Clair is located between Lake Huron and Lake Erie (42° 28’ N 82° 40’ W) and straddles the Canadian-U.S. border. The lake has a drainage basin of 13500 km², a surface area of about 1115 km², a mean depth of 3.4 m, and a maximum natural depth of 6.4 m, with a volume of 3.4 km³ (Leach, 1991). However, a navigation channel bisects the lake and has a depth of 8.3 m. The main inflow to the lake is via the St. Clair River with a mean monthly discharge of 5300 m³s⁻¹ (Derecki, 1984), which equates to 98% of outflow via the Detroit River (Leach, 1991). Other main tributaries include the Thames and Sydenham Rivers in Ontario, and the Clinton River in Michigan. The lake has a mean retention period of 9 days with a range of 2-30 days (Leach, 1991). Leach (1991) showed that there are two fairly discrete water masses occurring in the lake; a less productive North-western mass comprised primarily of Lake Huron waters, and a more productive South-eastern mass comprised mostly from the Ontario tributaries. The sediment of the entire south-eastern shoreline comprises a gravel-sand mix interspersed with areas of increased clay content (Rukavina, 1987). The lake does not undergo thermal stratification during the summer (Leach, 1991).

In recent years (1989-present), there has been a dramatic increase in aquatic macrophytes in Lake St. Clair. Distribution of macrophytes in Lake St. Clair increased from 326 km² (29% of lake surface area) of substrate in 1978 to 999 km² (90% of lake surface area) in 1995, with abundance of macrophyte beds of low density increasing from 198 to 513 km², medium beds increasing from 73 to 331 km², and high density beds increasing from 55 to 155 km² of substrate (Schloesser et al. 1997). These increases may potentially be linked to the introduction of zebra mussels, *Dreissena polymorpha* (Schloesser et al., 1997).
Large volumes of water filtered by *Dreissena* during feeding have been associated with reductions in phytoplankton biomass and productivity, with chlorophyll *a* values being reduced from 3.8 µg L⁻¹ (1988, pre-*Dreissena*) to values <0.7 µg L⁻¹ directly above mussel beds (Maclellan *et al.*, 1992). In Lake Erie, the reduction in phytoplankton, has in turn, led to an increase in water clarity with Secchi depth increasing 52% between 1988 (pre-*Dreissena*) and 1989 (post- *Dreissena*) (Maclellan *et al.*, 1992; Leach, 1993). This increase in water clarity relates directly to an increase in the amount of photosynthetically active radiation (PAR) available for aquatic macrophytes. Increased light penetration in the western basin of Lake Erie has led to increased aquatic macrophyte abundance and diversity in some littoral habitats (Stuckey and Moore, 1995). The ongoing changes in Lake St. Clair are similar to those in the western basin of Lake Erie and are consistent with a switch from a turbid, phytoplankton dominated state to a clear, macrophyte-dominated state. Such a shift and increase in macrophytes could alter both the biotic and abiotic environment in Lake St. Clair. In turn, these changes could potentially affect the abundance, growth, and survival of important fishery species, such as yellow perch.

**STUDY SPECIES**

Yellow perch are one of the most important commercial and recreational species in the Great Lakes system in North America. Total allowable catch for yellow perch during 1998 totalled, 6.57 million pounds for Lake Erie alone. Although there is no commercial fishery in Lake St. Clair, yellow perch remain one of the most utilised recreational species in the lake. Thus, it is vital for fisheries managers to be able to accurately predict growth and subsequent recruitment of yellow perch to these important fisheries.
Yellow perch are classified in the order Perciformes, family Percidae and binomial, *Perca flavescens*. There are two other species contained in the *Perca* genus, *P. fluviatilis*, the Eurasian perch, which is widely distributed throughout Europe and Asia, and *P. schrenki* Kessler, which is found only in parts of Russia (Craig, 1987).

Members of the Percidae exhibit plasticity in growth rates both spatially and temporally. In fact, both yellow perch and the congener European perch have widely varying growth rates depending on the wide variety of conditions they are exposed to locally or regionally (Keast, 1977; Boisclair and Leggett, 1989; Post and McQueen, 1994).

Yellow perch hatch at a length of approximately 4-7 mm total length (Craig, 1978; Powles and Warlen, 1988). During their early life history, yellow perch utilise a succession of different lentic habitats. Shortly after hatching, larval yellow perch migrate from the littoral zone to the pelagic zone where they have a relatively long pelagic larval phase (4-8 weeks). Once they reach an approximate size of 25-30 mm and age of 45-65 days, they go through an ontogenetic habitat shift back to the littoral or demersal zones (depending on lake size, depth, and stratification) for the remainder of their first growing season (Post and McQueen, 1988; Wahl et al., 1993).

Various explanations and triggers for this ontogenetic habitat shift have been put forth. For example, Kelso and Ward (1977) attributed the onshore migration at the end of the larval phase to predator avoidance in response to walleye predation. Whiteside et al. (1985) attributed the initial offshore migration to avoidance of littoral zone predators and the subsequent onshore migration to declines in pelagic zooplankton and an increased abundance of benthic invertebrate prey in the littoral zone. However, Post and McQueen (1988) noted that these migrations persist, despite prey and predator abundance in nearshore and offshore habitats that differ substantially between lakes. Wahl et al. 1993 showed that the shift from
pelagic to demersal habitats is coupled with increases in visual acuity to near adult levels. This increase in visual acuity is likely necessary to compensate for more cryptic benthic prey organisms, as well as decreased light levels associated with demersal habitats (Wahl et al., 1993).

**PURPOSE OF STUDY**

I speculate that the progressing shift in trophic status from a eutrophic to a more mesotrophic state and the associated increase in macrophytes could influence juvenile yellow perch diet and growth in Lake St. Clair. The purpose of this study was to utilise otolith microstructure to examine growth of YOY yellow perch, and determine if juvenile perch experience differences in growth between vegetated and non-vegetated habitats. The second chapter experimentally tests the ability of otolith microstructure to provide information on growth of YOY yellow perch. The purpose of the third chapter was to examine the diet and prey community available to YOY yellow perch and to use otolith microstructure to study growth of juvenile perch between highly vegetated and non-vegetated sites in Lake St. Clair. Information on growth of YOY yellow perch between habitats will allow fisheries managers to better estimate growth and recruitment of yellow perch in Lake St. Clair, and allow predictions of how populations of perch may react to continued increases in macrophyte production.
CHAPTER 2: Validation of Otolith Daily Growth Increments in Young-Of-Year (YOY) Yellow Perch (Perca flavescens) and Ability of Otolith Analysis To Predict Short-Term Effects of Food Ration on Growth.

ABSTRACT

Various factors including temperature, ration, and photoperiod have the ability to influence both daily otolith increment formation and the relationship between otolith size and fish size. I used 60 juvenile yellow perch (Perca flavescens) placed in 20 replicate 38 L aquaria and arranged in a randomised block design to a) validate daily increment formation in otoliths, b) determine if increment width relates well to short term changes in ration, and c) determine if there is a time lag associated with the response of otolith growth to changes in ration. Otoliths of all fish were marked with Oxytetracycline at the beginning of the experiment, and fish were placed in one of three treatment groups. Treatment groups included a control group (maximum ration throughout the course of the experiment), a max/min group (maximum ration for 10 d followed by maintenance ration for 10 d), and a min/max group (maintenance ration for 10 d followed by maximum ration for 10 d). Mean daily water temperature dropped from 18.9 °C to 14.9 °C during the course of the experiment and acted to mask changes in growth due to ration. There was no significant difference between the expected and observed number of daily increments for any treatment (p > 0.99). Mean increase in observed fork length of control group fish over the 29 d period (0.48±0.019 mm/d) was significantly greater than for the max/min (0.37±0.022 mm/d) fish, which showed significantly greater increases than the min/max fish (0.27±0.02 mm/d). Mean increase in fork length estimated from otolith increments was not significantly different from the observed values. However, estimated growth over the 20-d experimental ration period failed to show significant differences in growth among treatments. There appears to be a 1-2 d time
lag between change in ration and change in increment formation. However, there is no statistically detectable difference in growth until 5-10 d after a change in ration. These results indicated that otolith increment formation is daily in juvenile yellow perch and that the otolith-somatic growth relationship appears stable over a wide range of fish sizes and growth regimes. In addition, further studies on otolith analysis of juvenile yellow perch would probably achieve greatest resolution of changes in growth if they were based on taking average increment widths over a 10-day period.

INTRODUCTION

Otolith microstructure has been used to age fish since Reibisch (1899) first noted annual rings in the otoliths of plaice (*Pleuronectes platessa*). However, it was Panella (1971) who first observed that there were also intra-annual rings in otoliths, which roughly corresponded to the number of days in the year. Brothers *et al.* (1976) first verified that daily increments were indeed formed in lab-reared, larval anchovy (*Engraulus mordax*), and California grunion (*Leuresthes tenuis*). In addition for use in ageing, the fact that there is most often a strong relationship (either allometric or isometric) between otolith size and fish size (Jones, 1992; Neilson & Geen, 1982) means that width of daily increments can potentially be used to estimate daily somatic growth rates. If increment formation is in fact daily, then it is possible to back-calculate somatic growth at various times throughout the life of a fish. This ability to provide estimates of both age and growth makes the technique of daily ageing of otoliths a valuable tool in fish ecology, and has led to a steady increase in the number and type of research projects utilising otoliths (Jones, 1992; Campana, 1999). Since the early 1980's, use of otolith microstructure has been expanded to determine numerous aspects of fish life histories. Various authors have utilised daily increments to study age
structure (Campana and Moksness, 1991; Murphy et al., 1997), hatch date (Campana and Moksness, 1991; Moksness and Fossum, 1992), transition between life history stages (Antunes and Tesch, 1997; Fitzhugh et al., 1997), resource availability or environmental stress (Campana and Neilson, 1985; Rice et al., 1985; Jones and Brothers, 1987), mortality/survival (Methot, 1983; Post and Prankevicius, 1987; Al-Hossaini et al., 1989; Hoenig et al., 1990; Campana, 1996; Gleason and Bengton, 1996), as well as somatic growth rate (Al-Hossaini et al., 1989; Suthers & Sundby, 1993; Schirripa and Goodyear, 1997; Williams and Lowe, 1997; Suthers et al., 1999; Wang and Tzeng, 1999). For excellent reviews of otolith microstructure and microchemistry examination and analysis, see Stevenson and Campana (1992) and Campana (1999), respectively. All of these procedures rely on two key assumptions; a) that there are identifiable, annual or daily rings deposited in the otolith microstructure, and b) that there is a constant proportionality between otolith size and fish size throughout the life stage under observation (Campana, 1990).

The mechanism of formation of daily increments has been established for some time and involves the differential deposition of calcium carbonate and a protein matrix (Mugiya et al., 1981; Campana and Neilson, 1985; Mugiya, 1987). Each increment consists of both an incremental zone and a discontinuous zone. The broad, translucent, incremental zone primarily comprises crystalline calcium carbonate, while the thinner, more opaque, discontinuous zone is of a more proteinaceous origin (Campana and Neilson, 1985). Calcium carbonate makes up about 95% of the otolith structure, while the protein matrix composes approximately 3-4%, with 1% consisting of various trace elements.

Although the mechanism involved in incremental growth of otoliths is known, regulation of that mechanism can be influenced by a variety of factors. However, the daily periodicity most often observed in otoliths suggests that at least one of the factors that can
influence deposition rate must vary on a daily basis (Campana and Neilson, 1985). Campana and Neilson (1985) suggest that the control of daily increment formation is linked to an endocrine-driven, endogenous, circadian rhythm. They further suggest that this rhythm is entrained at an early age by photoperiod, and that additional factors such as temperature or diet can act to "mask" this underlying rhythm. This masking can occur either through addition of sub-daily increments, elimination of daily increments, or through reduction of increment width to a point where individual increments become indistinguishable. For an excellent review of the regulation processes of otolith growth, see Morales-Nin (2000).

Many studies have looked at factors influencing increment formation, including the three main ones of photoperiod, temperature, and diet. However, as Campana and Neilson (1985) point out, the results of various factors influencing increment formation can often appear contradictory, as well as species specific. For instance, absence of a 24 h light-dark cycle resulted in a lack of daily increments in green sunfish, Lepomis cyanellus, (Taubert and Coble, 1977) and mummichog, Fundulus heteroclitus (Radtke and Dean, 1982). However, other workers noted no inhibition of daily increment formation under either constant light (Campana and Neilson, 1982; Geffen, 1982) or dark (Neilson and Geen, 1982) conditions. Neilson and Geen (1985) were able to show that temperature on a 12 h cycle produced more than one increment per day in juvenile chinook salmon (Oncorhynchus tshawytscha). As well, cold temperatures resulted in the cessation of increment formation in sockeye salmon, Oncorhynchus nerka, (Marshall and Parker, 1982) and winter flounder, Pleuronectes americanus, (Casas, 1997). However, in an earlier paper, Neilson and Geen (1982) found that daily increment formation was maintained in chinook salmon, Oncorhynchus tshawytscha, at decreased temperatures, although increment width was reduced. Ration has been shown to either interrupt (Methot & Kramer, 1979; Geffen, 1982; Jones & Brothers,
1987; Al-Hossaini and Pitcher, 1988; Tzeng & Yu, 1992) or have no effect (Neilson and Geen, 1985; Maillet and Checkley, 1990; Molony and Choat, 1990; Paperno et al., 1997) on daily increment formation in otoliths. Zhang and Runham (1992) found that decreased temperatures disrupted daily increment formation in Oreochromis niloticus, but only when ration was also reduced.

In addition to influences on increment formation, various factors have been shown to influence the relationship between otolith size and fish size. If the relationship between otolith size and fish size changes during certain stages of a fish’s life, it could invalidate any subsequent back-calculations. Otolith growth is known to continue even under extreme conditions, and is considered conservative, in that there is no resorption of otoliths, as opposed to some other hard structures (e.g. opercula, scales) used in age and growth studies (Jones, 1992). These two facts can lead to an apparent ‘uncoupling’ of the relationship between otolith size and fish size. In most cases, the uncoupling appears to be the result of slow growth, brought on by factors such as metamorphic or ontogenetic transitions (Nishimura & Yamada, 1984; Hare & Cowan, 1995), or more commonly starvation (Marshall & Parker, 1982; Rice et al., 1985; Lagardere, 1989; Reznick et al., 1989; Secor and Dean, 1989; Szedlmayer, 1998). The uncoupling is characterised by slower growing (older) fish having larger otoliths, relative to faster growing (younger) fish of the same size. Slower growing groups of striped bass, Morone saxatilis, were shown to have larger and heavier otoliths than faster growing groups (Secor and Dean, 1989). However, using the same species, Dickey et al. (1997) found that otoliths of slow growing fish were not significantly larger than those of fast growing fish. They suggest that uncoupling may only occur in extreme circumstances. Reznick et al. (1989) showed that slowly growing guppies (Poecilia reticulata) had significantly larger otoliths than equal-sized, rapidly growing guppies. In this
case, the effect could only be attributed to changes in growth rate, since other factors such as temperature, genetics, and photoperiod were controlled for in the experimental design (Reznick et al., 1989). However, Mosegaard et al. (1988) observed an uncoupling associated with continually increasing otolith growth at hyperoptimal temperatures, where somatic growth decreased. They suggest that this may indicate a metabolic control of otolith growth.

At present, it is unclear what controls the mechanism of otolith growth, or why it may be so variably linked to numerous external factors. However, there is recent evidence that these factors may influence CaCO₃ deposition through changes in inner ear endolymph alkalinity and total CO₂ concentration, as opposed to total Ca and protein concentrations. Payan et al. (1998) indicate that starvation in rainbow trout (Oncorhynchus mykiss) did not change the composition of monovalent ions (Na⁺, K⁺, Cl⁻), total Ca, or protein concentration in the inner ear endolymph, suggesting none of these were involved with reduction in otolith growth associated with starvation. They conclude that the observed reduction in otolith growth was directly related to an overall reduction in the alkalinity of the endolymph, mediated by proton secretion. However, as Campana (1999) points out, a purely inorganic process such as the one outlined by Payan et al. (1997, 1998) cannot fully account for many of the features of otolith growth. To their credit, Payan et al. (1998) make a point of stating that their study only looked at overall protein concentrations, and could not discern qualitative changes in the proteins associated with otolith growth. Even though proteins make up a relatively small percentage of otolith structure, it appears they may play a pivotal role in calcification and otolith growth, and most likely control the rate of formation and type of calcium carbonate crystals in otoliths (Campana, 1999). There appears to be mounting evidence that otolith growth is strongly influenced by metabolic rate in fish, and not simply fish growth rate (Campana and Neilson, 1985; Mosegaard et al., 1988; Campana, 1999). It
is likely that this influence on metabolic rate ultimately controls the deposition rate of calcium and protein in the otolith (Campana, 1999).

Regardless of the exact control on the mechanism, it is obvious that numerous factors can potentially influence both increment formation and otolith growth. Therefore, it is essential that the daily formation of increments and the proportionality of the relationship with fish size is validated for each new species studied. In fact, Campana and Neilson (1985) note that it should be a prerequisite for any research based on otolith microstructure, regardless of previous work on the same species. The importance of validating daily increments becomes clear when you consider the numerous analyses that require adherence to the assumptions of daily increments and an allometric relationship between otolith size and fish size. Geffen (1992) reviews validation techniques and their importance for deposition rate, time of initial increment formation, relationship between otolith and somatic growth and the physiological mechanisms of deposition.

In general, the only direct methods of validating daily increment formation are a) to use fish of known age (often impossible in field situations), or b) to mark the otoliths in some manner at the beginning of an experimental period (Geffen 1992). Fish otoliths can be marked by inducing stress marks (or checks) within the otolith microstructure. These checks are visibly discernible from surrounding increments (Campana, 1992), and can be formed in the otoliths by inducing temperature stress (Mosegaard et al., 1988, Volk et al., 1999), starvation (Molony, 1996), U.V. radiation (Berghahn and Karakiri, 1990), anaerobic stress (Mugiya and Uchimura, 1989), photoperiod alteration (Wright, 1991), or physical stress (Campana, 1983). However, the most common method of marking otoliths has been with various fluorescent compounds including oxytetracycline, alizarin, and calcein (see Geffen,
1992 for a review). Once marked, direct counts of otolith increments after the experimental period will provide evidence for the presence or absence of daily increment formation.

In addition to validating daily increment formation, manipulative experiments coupled with otolith marking can elucidate what types of conditions may produce visible effects in the otoliths (Rice et al., 1985; Geffen, 1992). Geffen (1992) notes that factors such as temperature and feeding are more relevant to field situations than manipulations of photoperiod. Once their otoliths are marked, individual fish subjected to manipulations of ration or temperature can provide direct information on the relationship between increment width and somatic growth (Al-Hossaini and Pitcher, 1988; Molony and Choat, 1990; Geffen, 1992; Suthers et al., 1999). Direct manipulations will also provide evidence of any time lags between environmental influences and associated changes in otolith growth. Neilson and Geen (1985) noted a 3-week time lag before changes in increment width due to reduced rations were statistically detectable in juvenile chinook salmon, *O. tshawytscha*. Similarly, Molony and Choat (1990) observed a 15-day time lag between the beginning of an experimental starvation period and the corresponding response in otoliths of estuarine glass fish, *Ambassis vachelli*. In contrast, Paperno et al. (1997) found an immediate response in increment width of juvenile weakfish, *Cynoscion regalis*, in response to changes in ration.

The purpose of this study is to couple otolith marking with experimental manipulation of ration in young-of-the-year (YOY) yellow perch (*Perca flavescens*) in order to a) validate daily increment formation in otoliths, b) determine if ring width relates well to short term changes in ration, and c) determine if there is a time lag associated with the response of otolith growth to changes in ration.
MATERIALS AND METHODS

Source of Fish

For this experiment I used captive reared juvenile yellow perch. All fish were obtained from Stony Creek Equipment Co., a medium sized aquaculture operation located in Grant, Michigan. There were several reasons why I chose captive reared fish for this experiment. First, these fish were all adapted to feed on pellet food, which made rationing food much simpler and avoided having to acclimate wild fish to accept pellet food. Second, all fish were obtained from a single rearing tank, and although not all derived from a single pair of fish, they did represent a very small number of brood stock. This had the effect of eliminating at least some of the genetic variation that I would expect from wild stock. Third, all fish were hatched within the same week, so they were all essentially the same age. Thus age related growth changes should not have been a factor. Finally these fish were all acclimated to living at high densities, frequent handling, and living in confined habitats. All of these factors could have led to increased stress and thus, could have affected increment formation. For instance, Campana (1990) showed that handling stress can disrupt Ca deposition in otoliths of coho salmon, Oncorhynchus kisutch.

Materials

The experiment used 20 replicate 38 L glass aquaria. Each aquarium was supplied with dechlorinated water at a rate of approximately 0.5 L/min. Each aquarium was plumbed with a flow through siphon system that ensured constant water flow, and acted to remove any dissolved organic and nitrogenous waste. The siphon systems were constructed out of 1.25 cm, PVC tubing. Overall arrangement of aquaria, and design of the siphon can be seen in Plate 2.1a and 2.1b respectively. Each aquarium was further divided into three separate compartments with 2.5 mm plastic mesh (3M Plastic Canvas ©) (Plate 2.1b). This allowed
water flow between compartments but allowed separation of individual fish, thus allowing accurate application of rations to each individual fish. Sections of 10 cm diameter PVC pipe were cut in half and used in each compartment to provide cover and reduce stress in fish. Water temperature was recorded for the duration of the experiment using a Hobo Stowaway Submersible Temperature Logger programmed to record temperature at five minute intervals. Aquaria were also equipped with air pumps and air stones in case water flow was interrupted.

**Ration**

All fish were fed a commercial pellet food that consisted of 43% crude protein, and 8% fat. Food was purchased from Stony Creek Equipment Co. and was the food being fed to the perch at time of purchase. Any food remaining in the aquaria was removed after 8 hours.

To calculate daily rations for each fish, I used published equations based on aquaculture of Eurasian perch (Melard *et al.*, 1996). Since I wanted to study changes in increment width due to changes in ration, as opposed to starvation, I used the equations for maximum ration ($R_{\text{max}}$) and maintenance ration ($R_{\text{maint}}$):

$$R_{\text{max}} = 7.60w^{0.31} \quad R_{\text{maint}} = 1.09w^{0.23}$$

where $R =$ ration in % body weight/day.

However, these equations were calculated based on the optimal temperature for Eurasian perch growth of 23°C. Although yellow perch have been shown to have the same optimum temperature for growth (Schneider, 1973; Kitchell, 1977), I had no control over water temperature and my experiment ran at approximately 18°C for the first 10 days and 15°C for the last 10 days. To attempt to compensate rations for changes in metabolism associated with decreases in temperature, I reduced rations according to the bioenergetics model of
Kitchell et al. (1977) for yellow perch. Using their graph, which shows change in maintenance ration (gfood/gfish/day) with temperature, I was able to extrapolate the % change in maintenance ration associated with any particular change in temperature. I then applied this % change in ration to both my $R_{\text{max}}$ and $R_{\text{maint}}$ values. I calculated reductions in rations of 18% and 40%, for temperatures of 20°C and 15°C, respectively. Using these correction values, I was able to calculate a daily ration for each fish based on temperature and initial body weight. The relatively small weight gain expected in any particular fish over the course of the experiment did not seem large enough to justify the increased stress in re-weighing each fish to compensate ration for weight gains of fish.

**Experimental Design**

All fish were acclimated to laboratory water conditions in a 1900 L circular tank and fed *ad libitum* for one week. After the first week, all fish were held for 8 hours in an immersion bath of 700 mg/L Oxytetracycline (OTC) buffered with Na$_2$HPO$_4$ to incorporate a fluorescing band of OTC in their otoliths. Once marked, each fish was mildly anaesthetised and length and wet weight were measured. After a brief recovery period, fish were haphazardly placed, 3 per aquarium. Each fish was kept isolated with the use of partitions. Once in aquaria, the fish were acclimated and fed *ad libitum* for one week and then starved for 24 h prior to initiation of the experiment. The increased stress of starvation 24 h prior to the experiment, could form additional checks in the otoliths. These checks could then act as an alternative mark in otoliths if OTC was not incorporated into the otoliths of all fish.

Experimental groups consisted of two treatment groups and one control group. Fish in the first treatment group (max/min) were fed at $R_{\text{max}}$ for 10 days, then switched to $R_{\text{maint}}$ for 10 days. Fish in the second treatment group (min/max) were exposed to the opposite
regime of \(R_{\text{maint}}\) for 10 days followed by \(R_{\text{max}}\) for 10 days. Control fish were fed \(R_{\text{max}}\) for the entire 20-day experimental period. Assignment of groups was in a completely randomised block design, with each group represented once in each aquarium. After 20 days, all fish were fed \(R_{\text{max}}\) for an additional 2 days since it is often hard to discern the most recent 1-2 increments at the margin of the otolith. I expected the additional two days would allow for the entire experimental period to be interpreted in the otoliths.

All fish were euthanised with 10 mL of clove oil emulsified in 10 mL of 95% ethanol and mixed with 7 L of water. Measurements of fork length (FL), standard length (SL), and wet weight were obtained from each fish before being frozen for later dissection. Right and left lapilli were later dissected from each fish, cleaned of debris and tissue and mounted on glass slides using cyanoacrylate glue (Original KrazyGlue). Otoliths were then ground to the core using 3.0 and 0.3 μm lapping film (3M). Otoliths were viewed with a fluorescing scope at 400x and a digital image recorded the location of the fluorescing OTC band. Once the OTC band was identified, a light microscope with offset polarised filters coupled with a Coho, solid state video camera and SigmaScan image analysis system was used to count number of increments from otolith margin to the OTC band. SigmaScan was also used to measure the width of increments for the duration of the experimental period. All images of otoliths used in measurements were taken at 600x to ensure maximum resolution of the often narrow daily growth increments.

**Data Analysis**

All of the statistical analyses in this experiment were carried out using Systat Version 8.0 (standard version), Copyright SPSS Inc., 1998.
Water Temperature

To determine the effect of decreasing temperatures on increment widths during the experiment, regression was performed on control fish with mean 3-day water temperature as the independent variable and mean 3-day increment width the dependent variable. Only the control fish were used to perform this regression since they were the only ones to maintain the same ration (relative to temperature and body weight) throughout the experiment.

Daily Increment Validation

Since it is known that starvation or other severe stress can affect daily increment formation in some species, I compared observed and expected number of rings, post OTC exposure for each treatment. To determine if daily increment formation occurred, number of increments produced between the OTC fluorescent band and otolith margin from fish in each treatment were tested (Chi Square) against the expected number of increments based on days since otolith marking.

Effects of Ration on Growth

Otolith-Somatic Growth Relationship

To enable back-calculation of changes in fork length during the experiment, a regression of fork length on otolith radius was performed to determine the nature of the otolith radius-fish length relationship. This regression was also compared (using ANCOVA) to a regression previously calculated for wild fish from Lake St. Clair and Lake Erie. Since I only looked at a very narrow range of growth during this experiment, and since the regressions for wild and experimental fish showed minimal overlap in size range, only the regression model for the experimental fish was used to calculate estimated growth rates.
Observed and Estimated Growth

During the course of the experiment, fish in two aquaria escaped from the partitions within an aquarium. Since I was unable to discern which fish was receiving which treatment, these two aquaria (6 fish) were eliminated from all future analyses. In addition, one further aquarium (3 fish) was eliminated when otolith samples were mislabelled. Also, since not all otoliths were readable, a further four fish were eliminated from the analyses. To maintain the completely randomised block design, the entire block of fish associated with those four fish was also eliminated from further analyses. Thus, the total number of aquaria used in future growth analyses was 13, corresponding to 39 fish out of the original 60.

To ensure that there was no difference in the initial size of fish between treatments, I performed an analysis of variance (ANOVA) with initial FL as the dependent variable, treatment as the independent variable, and individual aquariams assigned as a blocking factor.

To determine if the change in ration actually produced a change in observed and estimated growth (FL) of experimental fish, I performed a two-factor ANOVA with growth (FL) as the dependent variable, and treatment and type (observed or estimated) as the independent variables. In this analysis, each aquarium was a blocking factor. An a posteriori Tukey HSD comparison was performed to determine which groups were significantly different from each other. Estimated mean increases in fork length over the 20-day experimental ration period were compared between treatments with a separate ANOVA. All growth data were tested for outliers and homogeneity of variance.
**Time Lags in Growth Response**

To try to obtain a more detailed picture of growth during the experimental period, and to identify any time lag between change in ration and change in growth, I first broke the 20 day period into two ten day periods representing the period before and after rations were switched. Estimated mean growth over each period was compared between treatments using an ANOVA with individual aquaria used as a blocking factor, treatment as the independent factor and mean growth over each period the dependent factor. In addition, the mean flux in growth between the two 10-day periods was compared between treatments with an ANOVA. The 20-day experimental period was further broken down into 5-day periods, including the 5 days prior to initiation of the ration experiment. ANOVAs were performed to compare mean growth between treatments for each 5-day period. This analysis combined with an examination of the change in daily increment width throughout the course of the experiment gave some idea of the presence or absence of a time lag between change in ration and subsequent changes in increment width, and fish growth.

**RESULTS**

**Water Temperature**

Water temperature declined over the course of the experimental period (Figure 2.1). Although initial mean water temperature was fairly high (18.9 ± 0.046 °C, mean ± se), the start of the experimental period coincided with a drop in mean temperature to 16.6 ± 0.23 °C (mean ± se). This was followed by a further drop to 14.9 ± 0.07 °C during the second 10 day ration period of the experiment.

Regression analysis of the mean 3-day growth and the mean 3-day water temperature for control fish during the 20 day experimental period was highly significant (F=21.665,
p=0.006). Growth declined with temperature in a linear fashion (Figure 2.2) and decline in temperature explained a large portion of the variance associated with decline in growth ($r^2=0.82$). The regression equation describing decrease in increment width with decreasing temperature for yellow perch was:

$$ \text{IW} = (0.197)\text{T} - 0.732 $$

where IW is increment width (μm) and T is temperature (°C). Since water was supplied via a flow through system and because of the complete randomised block design, all fish experienced the same water temperature regime throughout the experiment.

**Daily Increment Validation**

There was no significant difference between the observed and expected (29) frequency of otolith rings for any of the three ration treatments (Table 2.1). Thus, increment formation in yellow perch was daily under all ration treatments. The OTC bath was effective in establishing a visible fluorescent band in the otoliths of 72% (34) of the 47 yellow perch examined. The remaining 28% (13) of fish did not appear to incorporate OTC into their otoliths. However, it was readily apparent that the OTC band was associated with a very strong check in all otoliths where it was present (Plate 2.2). Nine of the 13 fish that did not show a visible OTC mark also had this distinct check mark in their otoliths. Thus, I used the check mark in those 9 fish to represent the initiation point of the 29-day post OTC exposure period. Two of the remaining four fish had otoliths that displayed neither the OTC band, nor the distinct check mark in the otolith, and were discarded. The remaining two fish had otoliths that were unreadable due to over grinding and irregularities in otolith structure.

**Effects of Ration on Growth**

**Otolith-Somatic Growth Relationship**
Regression of fork length on otolith radius was highly significant for experimental fish (F=230.7, p<0.001). The ability to predict fork length based on otolith radius was fairly high, as represented by an $r^2$ value of 0.83. This predictive value was slightly less than that for wild yellow perch previously studied from Lakes St. Clair and Erie ($r^2 = 0.92$). However, when the regressions were plotted (Figure 2.3) and compared via ANCOVA, there was no significant difference in the slopes (F=0.967, p=0.338) or the y-intercepts (F=1.105, p=0.296) of the two regression lines. The regression model used to estimate growth of experimental fish during the experiment was:

$$FL=(192.35)*(OR)-24.98$$

where FL is Fork Length (mm) and OR is otolith radius (μm).

**Observed and Estimated Growth**

There was no significant difference in the initial mean fork length (Figure 2.4) of any of the fish used in this experiment (ANOVA, F=0.406, df=2, p=0.67). The blocking factor of separate aquaria was not a significant factor in this analysis (ANOVA, df=12, F=0.399, p=0.95). Initial fork length was not used as a covariate in further analyses, since there was no detectable difference in initial fork length among treatments.

There was a significant difference in the observed and estimated growth of fish among treatments (Table 2.2) (Figure 2.5). As well, the blocking factor of separate aquaria was a significant factor in the overall analysis (Table 2.2). However, there was no significant difference between the estimated and observed growth for any of the treatments (Figure 2.5). This is indicated by the lack of a significant TREAT*GROWTYPE term in Table 2.2.

The mean increase in observed fork length of control fish was significantly greater than for the max/min fish, which showed significantly greater increases than the min/max fish (Figure 2.5). Observed growth was significantly different among all treatments when
compared with an. *a posteriori* Tukey HSD multiple comparison (Table 2.3). Mean daily growth of the control, max/min, and min/max treatments observed over the 29-day period were $0.48 \pm 0.019$, $0.37 \pm 0.022$, and $0.27 \pm 0.02$ mm/d (mean±se) respectively.

Estimated growth for fish in each treatment over the 29-day experimental period was very similar to the observed growth (Figure 2.5). Although there were no significant differences between observed and estimated values, it appeared that back-calculated growth for the min/max treatment may have been slightly over estimated. The estimated growth of only those fish in the control and the min/max treatments, were significantly different when compared with an *a posteriori* Tukey HSD multiple comparison (Table 2.3). The trend of decreasing growth from the control to max/min and then min/max treatments seen in the observed growth was still apparent in the plot of estimated growth (Figure 2.5). However, the differences between control-max/min and max/min-min/max treatments were not significant.

Estimated growth for the 20-day experimental ration period (Figure 2.6), showed similar trends to the observed and estimated growth over the 29-day period (Figure 2.5). However, there was no significant difference between estimated treatment means when tested with ANOVA (df=2, F=3.092, p=0.064). Based on a power of $1-\beta = 0.9$ and the associated variance and sample sizes, the minimum detectable difference between fork lengths for each treatment in this analysis would be 1.68 mm. This value is greater than the estimated mean difference seen between the control and the min/max treatment over the 20-day experimental period (1.34 mm).

**Time Lag in the Growth Response**

I was able to detect a difference between estimated mean growth of the control and min/max treatments during the first 10-day ration period (Figure 2.7a). The main treatment
effect was significant when tested with ANOVA (df=2, F=4.31, p=0.025) and an *a posteriori* Tukey HSD multiple comparison showed that the min/max treatment had significantly lower growth than the control treatment (Table 2.4). The min/max mean growth was also lower than the max/min treatment over the first 10 days; however, they were not significantly different (Table 2.4). The control and the max/min mean growth over the first 10 days were also not significantly different (Table 2.4). In addition, there was no significant difference between the mean growth of all treatments over the last 10 day ration period (ANOVA, df=2, F=4.307, p=0.147). Although not significant, it did appear that the two experimental treatments switched places, with the min/max treatment having slightly higher growth than the max/min treatment after the rations were switched (Figure 2.7a).

Although decreased temperature led to general decreases in growth of fish in all treatments, there was a significant difference between treatments in the magnitude of growth change between ration periods (ANOVA, df=2, F=3.598, p=0.043) (Figure 2.7b). When tested with an *a posteriori* Tukey HSD multiple comparison, the max/min treatment had a significantly greater decrease in growth between ration periods, than the min/max treatment (Table 2.5). The control treatment also appeared to have greater decrease than the min/max treatment (Figure 2.7b), although it was not significant. The max/min treatment also seemed to have a greater decrease in growth compared to the control (Figure 2.7b), but this change was also not significant.

Daily increment widths seemed to respond to changes in ration within 1-2 days (Figure 2.8a). Despite the relatively large variation in daily increment widths within each treatment, there were some apparent trends. First, there appears to be a sharp decrease in growth of the min/max treatment 1-2 days after they were switched to the maintenance ration on day 0. In addition, there is a sharp increase in increment width 1-2 days after they were
switched back to maximum ration on day 10. Increment widths in the min/max group remain similar to the control group over the last 10 days, when they were on the same ration (Figure 2.8a). Both the control and max/min groups remain relatively unchanged over the first 10-day period, while on the same ration. When compared to the control and min/max groups, the max/min group showed a decrease in increment width 1-2 days after they were switched from maximum to maintenance rations on day 10. However, this decrease was much less apparent than the decrease associated with the min/max group during the first 10 days. Additionally there was an overall decrease in increment widths for all treatments over the course of the experiment.

The same general trends that were apparent when looking at daily increments are apparent in the mean growth over 5-day periods (Figure 2.8b). However, using 5-day mean growth values decreased the variance associated with daily increment widths. I conducted separate ANOVAs to compare the mean growth values between treatments for each 5-day interval. It appears that growth of the control and max/min groups remains similar, but that the min/max group is considerably lower 5 days after the first ration switch, and that this difference is carried through the entire first 10 days (Figure 2.8b). However, the only significant difference between any of the treatment means, occurs between the control and min/max group during the 5-10 day period (Table 2.6 a & b). So although the change in increment widths seemed to lag by only 1-2 days, there was not a statistically detectable change in growth until 5-10 days into the reduced ration.
DISCUSSION

Water Temperature

The continuous decline in water temperature over the course of the experiment acted to partially mask the effects of ration shifts on the growth of juvenile yellow perch. The general trend of decreasing growth and increment widths over the course of the experiment could have two possible explanations. First, there is a general decrease in otolith increment widths that is associated with increasing age of fish (Campana, 1992; Molony, 1996; Molony and Sheaves, 1998). This effect was probably minimal in this case since the experiment ran for a relatively short duration. Second, there is also a general decrease in increment widths associated with decreasing temperature, and consequently, metabolic rates in fish. For example, Fitzhugh et al. (1997) found a decrease in mean widths of increments from >3 μm at 25°C to 1-2 μm at 15°C in Atlantic menhaden (Brevoortia tyrannus). A similar relationship was apparent here in the highly significant regression of mean 3-day growth on mean 3-day water temperature for control fish fed the same ration over the course of the experiment. This regression explained a significant amount of variation in 3-day mean growth ($r^2=0.82$). The remaining variation was probably related to both natural variation and that due to increasing age of fish. The percent ration was modified for all fish on day 10 of the experimental period; however, this had the effect of maintaining the maximum ration in relation to the declining temperature.

The low temperature and associated low growth rate of all fish during the last 10 days may have lead to my inability to identify changes in growth between the treatments during the last 10 days of the experiment. At temperatures close to the lower minimum required for growth, it is reasonable to assume that the low growth of all fish may have masked any change in growth due to changes in ration. This decrease in otolith increment width with
temperature is important, since it suggests that even fairly small differences in ambient water temperature could confound otolith based growth comparisons for yellow perch between habitats or between systems. Ideally, this experiment would have been conducted under a constant thermal regime. However, the fact that effects due to ration could still be determined under a decreasing thermal regime indicate that growth influences of temperature, if known, would not completely mask effects due to ration.

**Daily Increment Validation**

Increment formation in juvenile yellow perch was daily for all treatments over the course of the experimental period. This result is complementary to that of Powles and Warlen (1988), who found that daily increment formation commenced 1-3 days post-hatch in larval yellow perch and continued to at least the age of 35 days (length of study). Post and Prankevicius (1987) also showed that increment formation was daily in juvenile yellow perch from Dickie and St. George lakes (Ontario, Canada) over the first summer of growth.

Although increments were sometimes faint and difficult to distinguish in experimental fish, daily increment formation was apparent even after periods of stress, declining temperature, and reduced ration. This is consistent with several other studies that have researched the effects of changes in ration and temperature on otolith growth. For instance, Maillet and Checkley found that 1,2, or 3 days of starvation did not alter the daily periodicity of increment formation in Atlantic menhaden (*Brevoortia tyrannus*) larvae, although it did systematically affect width of growth increments. As well, Paperno *et al.* (1997) found that 6 ration treatments ranging from 17 to 100% maximum ration did not alter the daily periodicity of increment formation in otoliths of juvenile weakfish (*Cynoscion regalis*). However, they also found that ration did affect increment widths in a systematic fashion.
In contrast to these results, several other studies have shown a disruption in the daily formation of increments related to stress, ration, and/or temperature. For instance, Neilson and Geen (1985) found that diel cycles in water temperature could produce greater than 1 increment per day in juvenile chinook salmon (*Oncorhynchus tshawytscha*). These sub daily increments are now known to be common among many species, and are often associated with cyclic environmental variables (Campana, 1992). I observed very few sub daily increments in otoliths from experimental yellow perch. This is in contrast to wild fish from Lake St. Clair (chapter 3), which often show relatively distinct sub daily increments, and probably reflects the relatively stable environmental conditions experienced in the lab.

In addition to greater than daily increments, some researchers have shown less than daily increment formation under periods of reduced temperature. For example, Casas (1998) showed that winter flounder (*Pleuronectes americanus*) had less than daily increment formation at temperatures below 5 °C. As well, Marshall and Parker found less than daily increment formation in Sockeye salmon (*O. nerka*) at low temperatures. Zhang and Runham (1992) found that reduced temperatures only disrupted daily increment formation in *Oreochromis niloticus* in conjunction with reduced rations. However, all of these studies had temperatures lower than those seen here, and it is unlikely that the drop in temperature experienced over the course of this experiment was severe enough to influence daily increment formation. In addition, the decrease in temperature in my experiment did not drop below the lower limit (13.5 °C) associated with cessation of growth for yellow perch (Le Cren 1958, Nakashima and Leggett, 1975). Thus, it is not surprising that daily increment formation was maintained for the duration of the experimental period, despite a drop of approximately 5 °C over the course of the experiment.
Reduced rations and starvation also have caused less than daily increment formation in some species. Alhossaini and Pitcher (1988) showed that reduced rations produced less than daily increments in plaice (*Pleuronectes platessa*). Methot and Kramer (1979) showed that northern anchovy (*Engraulis mordax*) whose growth was severely reduced by reduction in rations had less than daily increment formation. However, they conclude that all sea-caught larvae grew fast enough to have daily increment formations. Zhang and Runham (1992) showed that low temperature combined with low rations were required to interrupt daily increment formation in *Oreochromis niloticus*. One thing common to these and other experiments showing less than daily increment formation is that they have either dealt with relatively severe conditions reflected by either complete starvation, long duration of reduced rations, or both. The shorter, 10-day period of reduced rations and decline in temperature in my experiment do not influence daily increment formation. These conditions are not unlike what most natural populations of perch are likely to experience throughout their first year of life.

Based on the fact that reduced rations and temperatures did not disrupt daily increment formation in older juvenile yellow perch in this experiment, and previous studies showing daily formation in early larval and juvenile perch (Post and Prankevicius, 1987; Powles and Warlen, 1988), it is reasonable to assume that under most natural circumstances otolith increment formation is daily in juvenile yellow perch. However, it should be noted that complete starvation or longer periods of reduced rations, may still have an influence on daily formation of increments. It is unknown how influential such severe circumstances would be in wild captured fish, since presumably most fish would have an increased mortality associated with periods of complete starvation or long periods of reduced ration.
Thus, fish surviving to time of capture are likely to comprise fish that have not undergone such severe conditions.

**Effects of Ration on Growth**

**Otolith - Somatic growth relationship**

The otolith radius, fork length relationship was highly significant for experimental fish. The high $r^2$ value allowed me to use otolith radius to back-calculate growth of fish during the treatment period. The relationship between otolith growth and somatic growth was the same for both wild fish captured from Lakes St. Clair and Erie during summer 1996 and farm-raised experimental fish. This result is important since it indicates that the relationship is stable for yellow perch over a wide range of YOY fish sizes, growth rates, and environmental conditions.

Any breakdown or uncoupling of this relationship within a species during certain life stages or due to extreme environmental stress would compromise the ability to accurately back-calculate growth from otoliths. Several studies have found an uncoupling of the otolith-somatic growth relationship within a species. Secor and Dean (1987) found that slower growing groups of juvenile striped bass (*Morone saxatilis*) had larger and heavier otoliths relative to fish length, than faster growing groups. As well, Reznick *et al.* (1989) found that slow growing guppies (*Poecilia reticulata*) had larger otoliths than equal-sized rapidly growing fish. Mosegaard *et al.* (1988) report similar uncoupling in Arctic char (*Salvelinus alpinus*) due to decreased growth caused by reduced temperatures. Most often, such uncoupling of the somatic-otolith growth relationship is associated with a severe stress to the fish. For example Dickey *et al.* (1997), also working on striped bass, found that slower growing fish did not have larger otoliths, and suggest that such uncoupling occurs only during periods of extreme circumstances.
Most studies showing uncoupling have also looked at larval or early juvenile fish. These smaller fish would have much lower energy stores compared to the larger juvenile fish I worked with. In addition, I used farm fish which had probably been exposed to maximum rations during their entire life, so had been able to build up plentiful energy stores. In addition to most energy being partitioned to somatic growth in young fish (Ehrlich, 1974), smaller juvenile and larval fish often have greatly increased metabolic demands compared to larger juveniles or adults. For instance, Post (1990) showed that larval and juvenile yellow perch active metabolism had the same weight dependent slope as adults but was 4.4 times adult standard respiration. Using model simulations, Post (1990) was able to show that consumption and growth dynamics of larval and juvenile perch are more sensitive to variations in temperature and prey availability than adults. Thus, it is probable that uncoupling of the otolith-somatic growth relationship is much more likely to occur in the larval or early juvenile phase during more extreme conditions, compared to larger juveniles studied here. This also implies that caution should be employed whenever early larval growth is back-calculated from larger juvenile fish.

**Observed Growth**

There was no significant difference in the initial size of yellow perch between treatments. Although initial fork length of fish ranged from 64-100mm, random placement into aquaria and treatments insured that there was no difference in the mean initial fork lengths of fish between treatments. This, and the fact that initial fork length was never a significant covariate, allowed me to directly compare growth between treatments.

The rations used over the course of the experiment did produce significantly different growth between treatments. Control fish fed the calculated maximum ration grew significantly more than both ration shifted treatments. Although both fed maintenance ration
for 10 days and maximum ration for 10 days, min/max fish grew significantly less than the max/min treatment fish. This observation is probably due to the combination of two factors. First, it is likely that fish fed on a low ration and then switched to a high ration are not able to realise equivalent growth, compared to fish fed on a high ration and then switched to a low ration. The reason for this is that the fish on the minimum ration first, have probably depleted a good portion of their energy stores and must then use part of the energy acquired during the subsequent high ration to replace energy stores. In contrast fish fed high ration first, can devote much more of the acquired energy to growth since they have not experienced the loss of energy stores. This result is similar to that of Tzeng and Yu (1992) who showed that even after starved larval milkfish (Chanos chanos) were fed for a 10 day period, their growth increments were still less than unity. They conclude that this indicates that the effect of starvation on growth increments extends beyond the period of starvation. Molony and Sheaves (1998) show that although adult Ambassis vachelli, showed recovery of viscera lipid, K-values, and otolith increment widths after periods of starvation, they did not recover to the same level present before starvation. They also note that increment widths were more conservative compared to the changes seen in Fulton’s K and lipid abundance. Second, this result was probably enhanced by the fact that temperature had dropped during the maximum ration period for the min/max treatment fish. Thus, reducing any compensatory growth even more. These two factors undoubtedly combined to produce the lower growth observed in the min/max treatment fish.

**Ability of Otoliths to Estimate Change in Growth**

Growth derived from back-calculation of otolith increments over the 29-day period accurately estimated the observed growth over the same period for each treatment. The estimated growth was not significantly different from the observed growth. However, an
interesting trend was that the estimated growth for the min/max treatment seemed to be somewhat overestimated. Although this value was not significantly different from the observed value, it may indicate that an uncoupling of the otolith-somatic growth relationship was underway. If that were the case, I would expect the regression model of fork length on otolith radius to overestimate the growth of slow growing fish. This result would be complimentary to results of others (mentioned above) who have recorded larger otoliths in slower growing fish. Further analysis of data from a separate experiment conducted by our laboratory, which involved extended periods on a maintenance ration, should be able to elucidate this result.

Although the estimated growth values were not significantly different from the observed growth, I was unable to distinguish a significant difference between the min/max and max/min fish using the estimated values. The main reason for this is that the large daily variation observed in the otolith increment widths translates directly to large variation in calculated growth rates. This large variation, coupled with a relatively small sample size (n=13) for each treatment, reduced the power of the ANOVA and increased the minimum detectable difference that the test was able to distinguish. Increased sample sizes most often present from natural populations would help to increase the power of the test.

This same problem of large variance and small sample sizes also led to the inability of the ANOVA test to distinguish a significant difference in estimated total growth between any of the treatment fish during the 20-day ration period. This problem was undoubtedly confounded by the effect of decreasing temperature to decrease overall growth rates of all fish.
**Time Lag in the Growth Response**

There appears to be only a 1-2 day lag time between change in ration and subsequent change in otolith increment width for juvenile yellow perch. However, estimated growth (based on increment width) did not show a significant change between treatments until at least 5-10 days after initiation of a ration change. Although the same trend of decreased increment widths (and thus growth) that is apparent in the daily increment widths is also apparent in the mean 5-day growth values, I could not detect any significant difference in growth between treatments until between 5 and 10 days after initiation of the first ration. Thus, although the response of otolith increment widths to change in ration appears to be fairly quick (1-2 days) and is apparent after only 5 days, I was unable to detect any difference until at least 5-10 days had passed. This result is similar to others who have looked at the time lag involved between change in rations and subsequent change in otolith increment widths. Molony and Choat (1990), found that a starvation treatment brought about a change in the increment width schedule of estuarine glassfish (*Ambassis vachelli*); however the actual pattern of the decline was not statistically apparent until between 10 and 15 days after commencement of the treatment. Similarly, Paperno *et al.* (1997) were able to observe a rapid change in increment width of juvenile weakfish (*Cynoscion regalis*); however there was a 7-day time lag before the change was statistically detectable. Molony and Sheaves (1998) suggest that this common time lag is associated with the fact that otoliths are maintained in a sacculus lined with macular cells that deposit calcium and otolin. They postulate that this provides a buffer from the supply of nutrients, oxygen, and energy in the blood stream and thus, reduces the effects of events like starvation on the width of increments.
Although I could not detect a difference in the growth of fish during the last 10 day period, I was able to show that the negative change in growth between the first and second ration periods, experienced by all treatments, was significantly less in the min/max treatment, compared to the max/min treatment. It was also less than the change in growth of the control group; however it was not significantly less. This reflects the trend for increment width to increase in the min/max fish during the last 10 days relative to the other two treatments. This suggests that although, all growth was reduced by temperature, the min/max fish showed some compensatory growth after the low ration period. Several studies have been able to show such compensatory growth after starvation or periods of low ration. Miglavs and Jobling (1989) observed increased food conversion efficiency and consumption rates after Arctic char (Salvelinus alpinus) were switched from restricted to satiation rations. Zhang and Runham (1992), showed similar compensatory growth evident in otoliths of Oreochromis niloticus after switching from both low temperature and low ration.
Plate 2.1 Photographs showing a) placement and layout of the 20 experimental aquaria with associated drainage system, and b) layout of an individual aquarium with mesh partitions and flow through siphon system. Inflow lines are located at the back of the aquaria.
Plate 2.2. Representative photomicrographs (400x) of a yellow perch (*Perca flavescens*) otolith. Arrows indicate a) oxytetracycline (OTC) band under UV light, and b) distinct check mark associated with the OTC band in the same otolith under normal light.
Table 2.1. Results of Chi-Square analysis comparing observed number of rings between OTC band (or check mark) and expected number (29) of rings based on daily ring formation since OTC marking of otoliths.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$X^2$</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.379</td>
<td>15</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Max/Min</td>
<td>0.345</td>
<td>14</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Min/Max</td>
<td>0.241</td>
<td>17</td>
<td>&gt;0.99</td>
</tr>
</tbody>
</table>
Table 2.2. Results of ANOVA for treatment means of observed and estimated growth over the entire 29-day post Oxytetracycline treatment period.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>176.88</td>
<td>12</td>
<td>14.74</td>
<td>2.37</td>
<td>0.014</td>
</tr>
<tr>
<td>Treat</td>
<td>355.50</td>
<td>2</td>
<td>177.75</td>
<td>28.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Growtype</td>
<td>13.40</td>
<td>1</td>
<td>13.40</td>
<td>2.15</td>
<td>0.147</td>
</tr>
<tr>
<td>Treat*Growtype</td>
<td>15.84</td>
<td>2</td>
<td>7.92</td>
<td>1.27</td>
<td>0.288</td>
</tr>
<tr>
<td>Error</td>
<td>373.27</td>
<td>60</td>
<td>6.22</td>
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<td></td>
</tr>
</tbody>
</table>
Table 2.3. Results of *a posteriori* Tukey HSD multiple comparison for treatment means of observed and estimated growth over the entire 29-day post Oxytetracycline treatment period. Matrix of pairwise comparison probabilities (df = 60). Observed = (O) Expected = (E).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control (O)</th>
<th>Max/Min (O)</th>
<th>Min/Max (O)</th>
<th>Control (E)</th>
<th>Max/Min (E)</th>
<th>Min/Max (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control (O)</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max/Min (O)</td>
<td>0.999</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min/Max (O)</td>
<td>0.411</td>
<td>0.212</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control (E)</td>
<td>0.040</td>
<td>0.014</td>
<td>0.869</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max/Min (E)</td>
<td>0.001</td>
<td>0.000</td>
<td>0.194</td>
<td>0.827</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Min/Max (E)</td>
<td>0.000</td>
<td>0.000</td>
<td>0.001</td>
<td>0.040</td>
<td>0.467</td>
<td>1.000</td>
</tr>
</tbody>
</table>
Table 2.4. Results of *a posteriori* Tukey HSD multiple comparison for treatment means of estimated growth over the first 10 days of the experimental period. Matrix of pairwise comparison probabilities (df = 24).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control</th>
<th>Max/Min</th>
<th>Min/Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max/Min</td>
<td>0.468</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Min/Max</td>
<td>0.020</td>
<td>0.217</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table 2.5. Results of *a posteriori* Tukey HSD multiple comparison for treatment means of estimated change in growth between first and second 10-day periods of the experiment. Matrix of pairwise comparison probabilities (df = 24).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control</th>
<th>Max/Min</th>
<th>Min/Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max/Min</td>
<td>0.640</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Min/Max</td>
<td>0.214</td>
<td>0.037</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table 2.6. Results of a) ANOVAs comparing treatment means of estimated growth for each 5 day period of the experiment, including the 5 day period prior to initiation of the first ration, and b) Matrix of Tukey HSD pairwise comparison probabilities (df = 24) for significant ANOVA model occurring at interval 5 to 10.

<table>
<thead>
<tr>
<th>Interval</th>
<th>F-ratio</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>-5 to 0</td>
<td>0.332</td>
<td>2</td>
<td>0.721</td>
</tr>
<tr>
<td>0 to 5</td>
<td>2.233</td>
<td>2</td>
<td>0.129</td>
</tr>
<tr>
<td>5 to 10</td>
<td>5.229</td>
<td>2</td>
<td>0.013</td>
</tr>
<tr>
<td>10 to 15</td>
<td>1.661</td>
<td>2</td>
<td>0.211</td>
</tr>
<tr>
<td>15 to 20</td>
<td>1.833</td>
<td>2</td>
<td>0.182</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control</th>
<th>Max/Min</th>
<th>Min/Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max/Min</td>
<td>0.293</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Min/Max</td>
<td>0.010</td>
<td>0.227</td>
<td>1.000</td>
</tr>
</tbody>
</table>
Figure 2.1. Mean daily water temperature (°C) showing temperature regime throughout the course of the experimental period, including days when ration was switched.
Figure 2.2. Regression of 3-day mean yellow perch otolith increment width (IW) (μm) on 3-day mean water temperature (T) (°C). $IW = (0.197)T - 0.732$, $r^2 = 0.82$, n=7.
Figure 2.3. Regression of Fork Length (mm) on otolith radius (mm) for experimental yellow perch (1998) and wild caught yellow perch from Lakes Erie and St. Clair (1996). Experimental fish model is FL=(192.35)*(OR)-24.98, \( r^2 = 0.83 \), n = 39.
Figure 2.4. Mean (± standard error) initial fork length (mm) of yellow perch for each treatment used in the ration experiment.
Figure 2.5. Observed and estimated mean (± standard error) increases in fork length (mm) of yellow perch over the 29-day experimental period for each treatment. Mean values with similar letters are not significantly different (A & B = estimated, C,D,&E = observed).
Figure 2.6. Mean (± standard error) increase in fork length (mm) of yellow perch during the 20 day experimental ration period for each treatment (no significant differences).
Figure 2.7. a) Mean (± standard error) growth in fork length (mm) of yellow perch for the duration of each 10 day ration period. Mean values with similar letters are not significantly different (A&B=0-10, C=10-20), and b) mean change in growth in fork length (mm) between the first and second 10 day ration periods.
Figure 2.8. a) Mean daily increment width for yellow perch otoliths during the 20-day experimental ration period. Vertical lines indicate days ration was switched. b) Mean growth in fork length during 5-day intervals throughout the experimental ration period. Arrows indicate means that are significantly different.

ABSTRACT

Recent increases in aquatic macrophyte distribution and abundance in Lake St. Clair, Ontario, have the potential to influence growth of important fishery species such as yellow perch (*Perca flavescens*). I examined prey community, diet, and growth of juvenile yellow perch from 3 vegetated and 3 non-vegetated sites in Lake St. Clair, Ontario during summer and fall of 1998 (July 3-9, Aug. 13-15, Aug. 27-28, and Sept. 24-Oct. 12). Benthic invertebrates were sampled using a Petit Ponar grab, zooplankton was sampled by a vertical tow of a 20 cm diam. (50 micron mesh) plankton net, and yellow perch were sampled with either a 15 m purse seine (July 3-9), an 8 m otter trawl (July 3-9), or fine mesh gill nets (August-October). In general, vegetated sites had higher densities of chironomids, amphipods, ephemeropterans, and trichopterans, while non-vegetated had higher densities of oligochaetes, nematodes, and *Hexagenia* mayflies. These patterns were reflected in the loadings of a discriminant function analysis that discriminated between vegetated and non-vegetated sites based on the invertebrate prey community. Zooplankton community was not used in this analysis since there was substantial sampling error associated with the samples. Juvenile yellow perch from both habitats fed predominantly on zooplankton during early July. Fish from both habitats switched to a benthic invertebrate dominated diet by late August. However, fish in non-vegetated sites continued to feed on zooplankton to a greater extent than fish in vegetated habitats. Although juvenile perch selected for similar organisms between habitats, diet also reflected the available prey community in each habitat. Mean size of fish was similar among the non-vegetated sites and the Lakeview vegetated site. Fish from the Mitchell’s Bay and Radio Tower vegetated sites were smaller than fish from non-
vegetated sites on all sample dates; however, this difference was not significant for the first two sample dates at the Radio Tower site. Growth rates standardised to fish size were not significantly different among all sites during the first two sample dates. However, fish from the vegetated Mitchell's Bay and Radio Tower sites had significantly lower growth rates than all other sites during the last two sample dates. Differences in both mean size and growth rates of yellow perch in the Mitchell's Bay and Radio Tower vegetated sites are most likely related to hatch date of the fish sampled and not habitat.

INTRODUCTION

In recent years (1989-present) there has been a dramatic increase in aquatic macrophytes in Lake St. Clair. Distribution of macrophytes in Lake St. Clair increased from 326 km$^2$ of substrate in 1978 to 999 km$^2$ in 1995 with abundance of macrophyte beds of low density increasing from 198 to 513 km$^2$, medium beds increasing from 73 to 331 km$^2$, and high density beds increasing from 55 to 155 km$^2$ of substrate (Schloesser et al. 1997). These increases may potentially be linked to the introduction and subsequent clearing of the water column by filter feeding activity of zebra mussels, *Dreissena polymorpha* (Schloesser et al., 1997). Such a shift and increase in macrophytes could alter both the biotic and abiotic environment in Lake St. Clair. In turn, these changes could potentially affect the abundance, growth, and survival of important fisheries species, such as yellow perch (*Perca flavescens*).

Several studies suggest that increases in aquatic vegetation, such as those observed in Lake St. Clair, may benefit yellow perch. Weaver *et al.* (1997) noted that yellow perch showed increased abundance and dominance where vegetation was abundant, species rich, and structurally complex. There is also strong evidence from literature on Eurasian perch, that suggests increasing aquatic macrophytes, may have beneficial impacts on yellow perch.
populations. Several studies have shown that young Eurasian perch preferentially choose vegetated over non-vegetated habitats (Coles, 1981; Wang and Eckmann, 1994; Rossier et al., 1996). In addition, perch seemed to be superior foragers in dense littoral vegetation when compared to several cyprinid species (Diehl, 1988). As well, Winfield (1986) noted that perch significantly increased their capture rate of *Daphnia magna* with increasing stem density of artificial vegetation, and had higher capture efficiency compared to roach at medium and high stem densities. Even though perch foraging efficiency probably improves over that of other species with increasing plant densities, there is likely to be a reduction in foraging efficiency at very high plant densities. Moss *et al.* (1998) showed decreased predation on *Daphnia hyalina* by perch in naturally high plant densities.

The general trend in most literature suggests that once yellow perch reach a size of approximately 35-40 mm in length, they will switch from a zooplankton-dominated diet to one increasingly dominated by benthic invertebrates (Hayes and Taylor, 1990). Several studies have shown that this switch to larger benthic invertebrate prey leads to increases in rates of perch growth. Hayes and Taylor (1990) found that perch able to switch to benthic prey of higher caloric value were able to grow more and delay maturity, allocating more energy to somatic growth, as opposed to perch restricted to a zooplankton diet. They also found that when benthic invertebrates were added to the diet of perch, the maximum size attained was substantially greater than for those feeding only on zooplankton, regardless of the age of first reproduction. Heath and Roff (1996) used a bioenergetics model to look at growth of stunted perch populations. They found that only the model with reduced benthic ration produced simulated growth parameters that matched the growth of perch in Lac Hertel, Quebec. They speculated that the relatively high proportion of cryptic benthic invertebrate species in this lake meant that most benthic prey items were unavailable to the visually
foraging perch. Additionally, Hayward and Margraf (1987) attributed the decline in growth of perch in the western basin of Lake Erie to a decline in larger bodied invertebrate prey organisms (e.g. *Hexagenia* and amphipods), relative to the central basins.

Despite the predominance of populations that show ontogenetic diet shifts from zooplankton to benthic prey, it is apparent that both the Eurasian perch and yellow perch are generalist foragers and are often able to utilise the most abundant prey items. Clady (1974) noted that yellow perch are able to utilise zooplankton if benthic prey is limited. Post and McQueen (1994) also showed that, in enclosure experiments, a diet shift from zooplankton to benthic prey was not necessary to sustain high growth rates. However, in several Ontario lakes, they did observe that cohorts that fed exclusively on zooplankton had slower growth rates relative to cohorts that experienced a diet shift to benthic prey. Diehl (1992) found that in the presence of macrophytes, age 2+ Eurasian perch fed on macroinvertebrates, but switched to zooplankton in the absence of vegetation. All of these studies, suggest that perch diet may fluctuate greatly between systems, depending on trophic status and available prey types. This, coupled with the importance of benthic invertebrate prey in diet ontogeny, suggests that the observed increases in macrophyte production and associated changes to the benthic community in Lake St. Clair, could influence growth of YOY yellow perch.

The purpose of this study was to examine both the prey communities and diet of YOY yellow perch in relation to growth, and determine if juvenile perch experience differences in growth between vegetated and non-vegetated habitats. Information on growth of YOY yellow perch between habitats will allow fisheries managers to better estimate growth and recruitment of yellow perch in Lake St. Clair, and allow predictions of how populations of perch may react to continued increases in macrophyte production.
MATERIALS AND METHODS

Site Selection

During spring 1998, I selected six sampling sites in Lake St. Clair, representing vegetated (Lakeview, Radio Tower, and Mitchell’s Bay) and non-vegetated (Maidstone, Belle River, and Stoney Pt.) habitat. Initially, sites were located with the need to ensure that the low number of replicate sites (3 per habitat type) would encompass a large portion of the lake. Once preliminary sites were located on a bathymetric map, I used S.C.U.B.A. to assess the suitability of each site. Once in the field, sites were selected based on broad criteria for vegetated vs non-vegetated substrate. Vegetated sites were required to have between 70 and 100% substrate occupied by plant cover, while non-vegetated sites were required to have less than 10% plant cover. A visual census of each site was conducted and macrophytes were identified to species level and percent coverage for each species was estimated using S.C.U.B.A. once during peak production (mid-August). The results of the census are provided in Appendix 1. Non-vegetated sites were also censused in this manner, to ensure that these sites remained free of aquatic vegetation throughout the study period. All sites had similar substrate composition, consisting of a sand-gravel mix interspersed with areas of increased clay content. This mix is identical to that described by Rukavina (1987) for the entire south-eastern shoreline of the lake. All sampling locations had depth profiles within the 2.5-4.0 m range. Sampling sites are mapped in Figure 3.1 and indicate whether the site was classified as vegetated or non-vegetated.

Sample Collection

All of the samples were collected on a biweekly basis. However, inability to catch fish, time constraints, and poor weather hampered the collection of required samples on
several sampling dates. Since many of the subsequent analyses were dependent on fish and benthic samples being collected concurrently, I only analyzed data from those dates where all samples were collected on the same dates. This reduced the number of sampling dates to four, comprising July 3-9, August 13-15, August 27-28, and September 24-October 12, 1998. In addition to biological samples, I recorded both temperature and depth for each site and sampling period. Water temperature remained relatively constant throughout the course of the study and the polymictic nature of Lake St. Clair ensured that temperatures remained the same among sampling locations (Table 3.1).

**Benthic Invertebrates**

I collected benthic invertebrate samples with a Petit Ponar benthic grab sampler, which sampled a 15x15 cm (225 cm$^2$) area. Triplicate grab samples were taken at each site on each sampling date (6 sites x 3 samples/site x 4 dates = 72 samples). Once retrieved, Ponar samples were placed into a 250 μm sieve bucket and rinsed to remove as much fine sediment as possible. Samples were then preserved with Kahle’s solution (15 parts 95% ethanol, 6 parts 100% formalin, 1 part glacial acetic acid, and 30 parts H$_2$O) and placed in large, plastic soil-sample bags for transport to the lab. Samples were stored in the soil bags and processed at a later date. Each sample was further washed and sieved through a series of 250, 500, and 1000 μm sieves to remove additional fine sediment and to separate large and small fractions. Each fraction was placed in a glass sample jar with 70% ethanol for future analysis.

Only those benthic samples corresponding to the four complete sample dates were used in subsequent analyses. Samples were examined under a stereo dissecting microscope and all invertebrates were removed and placed in vials containing 70% buffered ethanol for further processing. Once removed, I enumerated and identified benthic invertebrate samples
to Order or Family. Common, easily identified organisms such as the mayfly *Hexagenia* sp. and the mussel *Dreissena* sp. were identified at the genus level.

**Zooplankton**

I collected zooplankton samples with a vertical tow of a small, 20 cm diam. (50 µm mesh) plankton net. Samples were washed into 250 mL Nalgene bottles and preserved with a 5% formalin solution. Samples were then stored in the lab for later processing and analysis. The small diameter net was initially chosen for ease of sampling within dense aquatic plant beds. However, analysis of several samples revealed that the smaller plankton net had not adequately sampled the zooplankton community, resulting in many samples with either no zooplankton or only small bodied zooplankton present. Thus, I did not include zooplankton samples in the analysis of this study.

**Fish**

Early in the season YOY yellow perch were too small to be captured in gill nets and were sampled using two different techniques. All fish in the vegetated sites were collected with a 15 m purse seine. However, the purse seine was ineffective in catching fish in the non-vegetated sites, thus these sites were sampled with an 8 m otter trawl (25-mm coarse stretched mess with a 5 mm stretched-mesh cod end) towed for 10-15 minutes at approximately 4 knots. All subsequent fish samples were collected using four (2.5 x 8 m panel) fine-mesh gill nets (either 8 or 16-mm stretched mesh). Fish samples were immediately placed on ice and subsequently frozen upon return to the lab. Once thawed, all fish were measured to the nearest 1 mm and weighed to the nearest 0.1g wet weight. Previous work in the lab had shown that yellow perch experience an approximate 2.0% shrinkage when frozen from 1-6 months. Thus, all fish lengths were corrected for shrinkage.
and represent fresh length. Once measured and weighed, fish stomachs were excised and preserved in a 5% buffered sugar formalin solution for later diet analysis.

Right and left lapillus otoliths were also dissected from each fish, cleaned of debris and tissue, and either stored in glass vials containing 95% buffered ethanol, or mounted on glass slides using cyanoacrylate glue (Original KrazyGlue). Otoliths were then ground to the core using 3.0 and 0.3 μm silica-carbide lapping film (3M St. Paul, MN), cleared with a drop of immersion oil, and viewed at 400-600x on a Nikon light microscope with offset polarising filters and coupled with a Coho, solid state video camera. Otolith images were saved and SigmaScan Pro 5.0 (Copyright SPSS Inc., 1999) image analysis system was used to analyse all otolith images.

**Data Analysis**

All of the statistical analyses in this experiment were carried out using Systat Version 8.0 (standard version), Copyright SPSS Inc., 1998.

**Benthic Invertebrates**

To determine if the composition of the benthic invertebrate community was predictive of the state of vegetation at a site, I first plotted mean numbers of organisms for sites pooled as vegetated and non-vegetated sites. I then performed a Discriminant Function Analysis (DFA) on the benthic invertebrate data. With only two groups, DFA is analogous to multiple regression. However, DFA allowed me to examine the question of whether benthic invertebrate composition varied in a manner that was predictive of the vegetation-state of a site. To maintain the recommended ≤ n-2 number of predictor variables (Tabachnick and Fidell, 1996), I first pooled the triplicate site data into vegetated and non-vegetated groupings. Based on preliminary diet analysis I was further able to reduce the number of variables to the 6 groups of organisms found in at least 10% of all perch stomachs.
Thus, the DFA essentially tested whether the numbers of potential prey items varied in a manner that was predictive of the vegetation-state of a site. Normal probability plots were constructed for each variable to ensure normality and lack of significant outliers.

**Fish**

**Catch-Per-Unit-Effort (CPUE)**

CPUE graphs were constructed for each site at each date as a surrogate measure of fish density. A variety of techniques were used to capture YOY yellow perch during the early July sample. Thus, CPUE was not calculated for these samples since the units were not comparable among sites. For all subsequent dates, CPUE was calculated for gill nets as number of YOY yellow perch captured per 8 x 2.5 m panel per hour of net deployment.

**Diet Analysis**

Most YOY yellow perch stomach contents were poorly preserved. Despite being put on ice immediately after capture and frozen within 3-4 hours, most stomachs contained very few identifiable organisms. In addition, remaining diet data was somewhat limited by the relatively low sample sizes and poor quality data. These two factors precluded me from performing the planned individual-based examination of the relationship between diet and growth. Despite low sample sizes, I did examine if diet of perch differed between vegetated and non-vegetated sites. I first pooled the proportion of organisms in diet for perch from each habitat and graphed for each sampling date. I was then able to calculate Chesson’s alpha selectivity index for benthic organisms:

\[ \alpha = \frac{r_i / n_i}{\sum_{j=1}^{m} r_j / n_j} \]

Where \( r_i \) is the number of items of food type \( i \) in the consumer’s diet and \( n_i \) is the number of items of food type \( i \) in the environment. The \( r_i \) and \( n_i \) can be expressed as the proportion or
percentage of food type $i$ in the diet and environment, respectively (Chesson, 1983). Chesson's alpha index does not change with food density unless consumer behaviour also changes (Chesson, 1978; Chesson, 1983). Once calculated, I graphically compared Chesson’s alpha index for preference of certain benthic invertebrates between fish feeding in vegetated habitats and fish feeding in non-vegetated habitats.

**Fish Growth**

The mean of the last 10 days of otolith daily increments was utilised to compare recent growth in yellow perch among sites. The last 10 growth rings in yellow perch otoliths represent the last 10 days of growth prior to capture, and probably reflects the habitat that the fish was caught in. In addition, a mean of a 10-day period incorporates a sufficient group of measurements to smooth out increased variance associated with looking at daily growth (refer to Chapter 2). To enable back-calculation of growth during that 10-day period, a regression of fork length on otolith radius was performed to determine the exact nature of the otolith radius-fish length relationship in YOY yellow perch. The radius of the $10^{th}$ increment from the edge was then used to calculate the fork length of the fish 10 days prior to collection and thus growth of the fish over the 10-day period. The otolith-fork length regression was also compared (ANCOVA) to a similar regression calculated for the experimental fish in Chapter 2.

Additional work conducted by our laboratory, in conjunction with this research, indicated that hatch dates for the 1998 year class of yellow perch in Lake St. Clair were protracted over a 10 week period and consisted of an early and late mode (Fitzgerald et al. 2000). Depending on hatch date, cohorts of early or late hatched fish may encounter less favourable growth conditions (e.g. decreased food availability, temperature, increased predation pressure) compared to alternate cohorts. Thus, regressions of otolith radius on fork
length for fish representing early and late hatch dates were compared via ANCOVA to determine if hatch date affected the otolith-somatic growth relationship.

I assessed the potential for fluctuating asymmetry (Somarkis et al., 1997) to confound daily growth rates by measuring growth from both the left and right lapillus in a set of 50 individual fish. There was no significant difference ($p = 0.156$) between growth rates calculated from the left or right lapillus when compared with a paired t-test. Therefore, I was able to use either the left or right lapillus for calculating growth rates in YOY yellow perch.

Growth in fish is generally considered to be size dependent, although part of that dependency is on age, as well as size itself. The fact that growth can vary due to size (i.e. larger fish grow slower than small fish) can hinder the comparison of growth rates among populations that have significant size discrepancies. To determine if size of fish differed between sites, I performed an analysis of variance (ANOVA) for each sampling date, with fork length at capture as the dependent variable and site as the independent variable. If the overall ANOVA was significant I performed an a posteriori Tukey HSD comparison to determine which sites were significantly different from each other. Significant differences in fork length among sites led me to calculate a growth rate standardised for size of the fish. To accomplish this, I performed a regression of mean daily growth rate on fork length for all fish pooled together. I then calculated a predicted growth rate based on the size (FL) of the fish alone. To standardise the growth rate to the size of fish, I subtracted the growth rate predicted from size of the fish from the 10-day growth rate. The resultant growth rate was thus standardised for all fish sizes, and allowed me to directly compare growth rates among sites, regardless of size differences in fish. These standardised growth rates were then compared among sites for each date via ANOVA with size-standardised growth as the dependent variable and site as the independent variable. I then performed an a posteriori
Tukey HSD comparison to determine which sites were significantly different from each other. All growth data were tested for outliers and homogeneity of variance.

RESULTS

Benthic Invertebrates

For all sampling dates, the vegetated sites had a substantially higher density of chironomids, compared to non-vegetated sites (Figure 3.2 and 3.3). Relative mean densities remained similar for both sites throughout the sampling season. Non-vegetated sites had consistently higher densities of *Dreissena polymorpha* than vegetated sites. However, it should be noted that the vegetated sites had substantial numbers of newly settled *Dreissena* recruits present in all samples from mid-August until late September. In fact, these newly settled individuals were present in such high numbers that it was impractical to try to count them. Nevertheless, the density of adult *Dreissena* remained very low for all vegetated sites. Vegetated sites had slightly higher densities of Amphipods as well as Ephemeroptera and Trichoptera for all sampling dates (Figure 3.2 and Figure 3.3). Non-vegetated sites generally had slightly greater densities of both Oligochaetes and Nematodes throughout the sampling season.

Discriminant function analysis based on inclusion of the 6 most important prey items present in the environment produced a Discriminant root with high Canonical r values for all sampling dates (Table 3.2). As well, the overall test of whether benthic organisms discriminated between vegetated and non-vegetated sites was highly significant for all sampling dates (Table 3.2). For July samples, chironomids, amphipods, trichopterans, and ephemeropterans, all loaded negatively, while *Hexagenia* and Oligochaetes loaded positively. This relates to the negative and positive loadings of the vegetated vs non-vegetated sites.
This general pattern persisted throughout the season and suggests that the benthic invertebrate prey community differed in a predictable fashion between vegetated and non-vegetated habitats.

**Fish**

**Catch-Per-Unit-Effort (CPUE)**

Mean CPUE was much higher for fish captured in vegetated sites during the mid-August sample (Figure 3.4a), indicating higher densities of fish in the vegetated sites. However, when the CPUE was separated into individual sites, it is apparent that the large CPUE was mostly associated with the Mitchell’s Bay and Radio Tower sites (Figure 3.4b). These two sites had generally higher CPUE for each sampling date while the CPUE at the third vegetated site (Lakeview) was similar to all non-vegetated sites for each sampling date.

**Diet Analysis**

Unfortunately, poor initial preservation of stomach content data rendered much of the diet analysis ineffective. In addition, I did not feel that the quality of the diet data justified trying to determine multivariate links between the diet of individual fish and their growth rate over the last 10 days. However, despite low sample numbers and poor quality data, I was able to draw some inferences about YOY yellow perch diet between habitats.

Early July data showed a high degree of similarity in proportions of organisms in diet of yellow perch from vegetated and non-vegetated sites (Figure 3.5a). The vast majority of diet for fish in each habitat comprised Copepods, Cladocera, and other zooplankton. A very small percentage of the diet of fish in the vegetated habitat consisted of chironomids (Figure 3.5a). By mid August, dependence on Copepods was declining in fish from both habitats and fish in each habitat had started to switch to feeding more on benthic invertebrates (Figure
3.5b). *Dreissena polymorpha* were not included in any of the diet graphs since they were not found in any of the perch stomachs.

By late August, a switch towards more benthic prey was obvious in fish from both vegetated and non-vegetated habitats (Figure 3.6a). However, fish in non-vegetated sites retained a higher proportion of zooplankton in their diets, and seemed to be including a higher proportion of large bodied zooplankton (Cladocera and Rotifera) compared to earlier samples (Figure 3.6a). Fish in non-vegetated habitats also had a higher proportion of oligochaetes and *Hexagenia* in their diet. This probably reflects the higher proportion of these organisms in the non-vegetated sites. Perch in vegetated sites appeared to be switching prey from smaller bodied zooplankton to larger bodied benthic invertebrates, including Ephemeroptera, Trichoptera, Amphipoda, and particularly Chironomidae (Figure 3.6a).

By late September, fish in both habitats were feeding predominantly on benthic organisms (Figure 3.6b). Fish in non-vegetated sites were still feeding on rotifers, but had also included a larger percentage of *Hexagenia*, oligochaetes, and chironomids in their diet (Figure 3.6b). Fish in vegetated sites had similar proportions of Ephemeroptera, Trichoptera, Amphipoda, and Chironomidae to those seen in the late August data (Figure 3.6b), suggesting that their diet may have stabilised somewhat.

Chesson’s alpha calculated for benthic invertebrates suggests that during mid-August, fish in both habitats had a strong preference for *Hexagenia* (Figure 3.7a) despite their relatively low numbers, especially in the vegetated sites. In addition, fish in non-vegetated sites showed strong preference for amphipods. Fish in vegetated sites also showed relatively strong selection for both Ephemeroptera and Trichoptera. However, neither group of fish showed an overly strong preference for chironomids, although these organisms composed a substantial portion of their diet. During later sampling dates, fish from both sites
showed increased preference for Ephemeroptera, other than *Hexagenia*. However, fish from both sites still show selection for *Hexagenia* in both late August and late September (Figure 3.7 b & c). Fish in vegetated habitats selected for gastropods during late August but this was reduced in late September. The lack of any selection for Coleoptera by fish in non-vegetated sites reflects the fact that these organisms were not present in the non-vegetated sites.

**Fish Growth**

Regression of fork length on otolith radius was highly significant for YOY yellow perch from Lake St. Clair during 1998 (F=7282.9, p<0.0001). The ability to predict fork length based on otolith radius was very high, as represented by an $r^2$ value of 0.95. Although a second order polynomial regression of the data produced a significantly better fit than the linear regression (Table 3.3), the resulting model severely underestimated growth of small fish. A consequence of this poor fit for small fish was that the y-intercept of the curvilinear regression indicated that fish of approximately 20-25 mm would have an otolith radius approaching 0. Thus, the linear regression was used in this study to estimate mean daily yellow perch growth over the last 10 days. The predictive value of the linear regression was higher than that for experimental fish in Chapter 2 ($r^2=0.83$). However, when the regressions were plotted (Figure 3.8) and compared via ANCOVA, there was no significant difference in the slopes (F=0.888, p=0.346) or the y-intercepts (F=0.364, p=0.546) of the two regression lines. The regression model used to estimate growth of experimental fish during the experiment was:

$$FL=(179.1)*(OR)-19.81$$

where FL is Fork Length (mm) and OR is otolith radius (µm).

Yellow perch identified as belonging to a late-hatched cohort showed a significant difference between the slopes (F=48.07, p<0.001.) and y-intercepts (F=40.05, p<0.001) of
the relationship of otolith radius and fork length compared to the cohort of fish representing the early hatch date (Figure 3.8). However, it should be noted that the late-hatched cohort is represented by fish spanning a very narrow size range of fish in the middle of the overall size distribution. These fish also seem to fall well within the variation occurring for early hatched fish of the same size. In fact, comparison of regression lines (ANCOVA) of fork length on otolith radius, reveals that the slopes (F=1.788, p=0.183) and y-intercepts (F=1.041, p=.309) are not significantly different between late and early hatched fish of the same size.

Regression of mean daily growth rate on fork length was also highly significant for YOY yellow perch from Lake St. Clair during 1998 (F=53.29, p<0.001). As expected, the ability to predict daily growth based solely on fork length was low, as represented by an r-square value of 0.16 (Figure 3.9). However, knowledge of this relationship allowed me to account for changes in growth associated with size of fish when comparing growth rates between sites that have fish of significantly different sizes. The regression model used to standardise daily growth of yellow perch to fish size was:

\[
\text{Growth}=(-0.005)\times(\text{FL})+0.861
\]

where FL is Fork Length (mm) at time of capture.

When comparing mean fork lengths and standardised growth rates among sampling sites, an *a posteriori* Tukey HSD comparison was conducted in all cases where the main ANOVA effect was significant. However, to avoid excessive use of tables containing the associated statistics and p-values from the Tukey tests, means that were not significantly different (i.e. p-value >0.05) were connected with a line in Figures 3.10-3.13.

During early July, mean length of fish was significantly different among the four sites where fish were caught (ANOVA, df =3, F=16.23, p<0.001). The mean fork length of fish
from Belle R. was significantly greater than for fish from both vegetated sites but not the other non-vegetated site (Figure 3.10). Fish from Stoney Pt. were significantly larger than fish from Mitchell’s Bay, but not larger than fish from Radio Tower. In fact, fish from Mitchell’s bay were significantly smaller than all other fish sampled in July. However, although a similar pattern is seen, there is no significant difference in the standardised growth rates among sites (ANOVA, df =3, F=2.323, p=0.084) during July.

A similar pattern is seen in mid-August (ANOVA, df =5, F=14.08, p<0.001), in that fish from Mitchell’s bay remained significantly smaller than fish from any other site (Figure 3.11a). In general, fish from the non-vegetated sites tended to be significantly larger than fish from the vegetated sites. However, this difference was not always significant (Figure 3.11a). When mean daily growth rates were standardised for differences in the mean length of fish among sites, there was no significant difference in growth among any of the sites (ANOVA, df =5, F=0.836, p=0.528).

During late August, there was an even more pronounced difference in the size of fish among sites (ANOVA, df =5, F=54.41, p<0.001), with fish from the vegetated sites of Mitchell’s Bay and Radio Tower being significantly smaller than those fish from the other four sites. However, fish from the third vegetated site (Lakeview) had a similar mean fork length to the fish from non-vegetated sites, although they were still significantly smaller than fish from Maidstone (Figure 3.12a). In addition to being significantly smaller, fish from Mitchell’s Bay and Radio Tower also showed significantly lower growth rates compared to fish from all other sites (ANOVA, df =5, F=27.36, p<0.001)(Figure 3.12b).

Continuing into late September there was still a significant difference in fork lengths among sites (ANOVA, df =5, F=39.33, p<0.001). The same pattern observed in late August carries over into late September with fish from the vegetated sites of Radio Tower and
Mitchell’s Bay being significantly smaller than fish from all other sites (Figure 3.13a). Fish from the vegetated Lakeview site show no difference in mean size from the 3 non-vegetated sites (Figure 3.13a). Additionally, fish from Radio Tower and Mitchell’s Bay continued to have a significantly lower growth rate than fish from all other sites in late September (ANOVA, df =5, F=7.00, p<0.001)(Figure 3.13b).

DISCUSSION

Benthic Invertebrates

There were substantially higher densities of chironomid larvae present in vegetated sites compared to non-vegetated sites in Lake St. Clair during 1998. In addition there were generally higher densities of Trichoptera and Ephemeroptera in the vegetated sites. It was apparent that benthic invertebrate prey community was also richer in the vegetated sites as compared to non-vegetated sites. These results support the work of other researchers who have seen increases in both densities of individual organisms as well as increased diversity and richness of benthic organisms associated with aquatic macrophytes. For instance, Diehl (1988) found increased chironomid densities associated with aquatic vegetation in both field and lab experiments. Diehl (1988) was able to use laboratory habitat preference experiments to show that that chironomids preferred vegetated areas over non-vegetated areas. Cyr and Downing (1988) found that the abundance of invertebrates was best related to the biomass of separate plant species.

Non-vegetated sites in Lake St. Clair had consistently greater densities of zebra mussels (*Dreissena polymorpha*) than the vegetated sites. There was a large number of newly settled zebra mussels present in both the vegetated and non-vegetated sites during the late August and late September sample dates. The number of settled juvenile mussels was
higher in vegetated sites; however, the number of large adult mussels was very low for all vegetated sites during all sample dates. This suggests that although the increased structural complexity of aquatic macrophytes may offer an attractive settlement substrate, their long-term suitability as habitat for zebra mussels, is probably quite poor. This makes inherent sense, since the plants senesce and break down during the fall and winter, thus destroying the habitat that the mussels first settled on. This large seasonal disturbance of the aquatic macrophyte populations probably accounts for the fact that zebra mussels do not appear to be able to successfully inhabit heavily vegetated areas.

In addition to zebra mussels, non-vegetated sites generally contained higher densities of oligochaetes, nematodes, and the mayfly, *Hexagenia*. This trend of increased numbers of oligochaetes and nematodes is similar to what is generally seen once zebra mussels inhabit an area. In particular, Griffiths (1993) notes that the increased abundance of amphipods, flatworms, and snails associated with zebra mussel colonisation of Lake St. Clair is probably due to the altered habitat structure brought about by the presence of zebra mussels. In addition Griffiths (1993) notes that the deposition of faeces and pseudofeces is the likely reason for the increase in abundance and richness of various worm species. The slightly higher densities of *Hexagenia* present in the non-vegetated sites is most likely related to their avoidance of vegetated sites as opposed to an indirect enhancement effect of zebra mussels. Rasmussen (1988) found that suitability of sites for colonisation of *Hexagenia* was negatively related to the abundance of submerged macrophytes, especially if high macrophyte biomass was developed near the substrate.

**Diet**

Diet of YOY yellow perch in July showed a high degree of similarity across sites with the vast majority of diet consisting of copepods, cladocerans, and other zooplankton.
However, this dependence on zooplankton started to decline in August and there was an apparent ontogenetic shift from zooplankton to benthic organisms over the summer. This result reflects the general trend suggested in most literature depicting an early importance of zooplankton in perch diets followed by a switch to larger benthic invertebrate prey once zooplankton populations change or are depleted (Hayes and Taylor, 1990). For instance, Wu and Culver (1992) found that YOY yellow perch in Western Lake Erie switched from feeding on zooplankton to benthic prey after a mid-summer decline in zooplankton abundance. Synnestvedt (1997) noticed very similar patterns of diet and ontogenetic diet shifts in YOY yellow perch in Anchor Bay, Lake St. Clair.

Although all fish from both the vegetated and the non-vegetated sites showed a switch towards benthic prey, the fish in the non-vegetated sites continued to prey upon larger bodied zooplankton longer into the season than fish from the vegetated sites. Unfortunately, lack of data from the zooplankton samples in this study precludes any interpretation as to whether these larger bodied zooplankton are simply more abundant in the non-vegetated sites, or if they are better able to avoid predation in the vegetated sites by using the macrophytes as a refuge. For example, Lauridsen and Lodge (1996) showed that *Daphnia magna* exhibited a chemically mediated increase in its occupation of aquatic macrophytes when exposed to fish or fish odours. In addition, Scheffer (1993) points out that macrophyte refuges for *Daphnia* and other large bodied zooplankton contribute significantly to the high *Daphnia*-low phytoplankton-high macrophyte state in shallow lakes.

By late September, all fish have switched almost entirely to benthic invertebrates in their diet. Although the benthic community was shown to differ between vegetated and non-vegetated sites, YOY yellow perch appeared to have the ability to include a variety of benthic invertebrates into their diet.
Fish in both habitats showed a preference for the mayfly *Hexagenia* during August. Although the abundance of *Hexagenia* was relatively low for all sites, YOY perch were obviously selecting these organisms. The importance of *Hexagenia* in yellow perch diet is highlighted by the fact that when low oxygen conditions linked to excessive nutrient loading in Lake Erie caused the decline of *Hexagenia* populations, yellow perch in that lake were shown to undergo a resultant decline in consumption rates coupled with stunting of growth (Hayward and Margraf, 1987). The large increase in the preference by YOY yellow perch for other members of Ephemeroptera was probably related to the high food-quality of these prey items. The general selection for amphipods by both groups of fish supports the results of Synnestvedt (1997) who showed that YOY yellow perch fed almost exclusively on amphipods in Anchor Bay, Lake St. Clair during late summer and early fall.

Diet analysis in this study was severely hampered by poor preservation of gut contents. In previous studies conducted on yellow perch in our laboratory were able to either place fish directly in a preservative or inject preservative directly into the body cavity of individual fish. However, examination of the otoliths of fish that had been previously stored in or injected with a variety of preservatives indicated that the preservatives in all of these methods damaged the otoliths, rendering them unreadable. The importance of obtaining both diet and growth data from individual fish warrants further refinement of techniques to allow for adequate preservation of stomach contents while still allowing use of the otoliths to determine growth rates. A possible method of avoiding this problem would be to dissect fish in the field and store stomach and otolith/whole fish samples separately. Additionally, a field based form of gastric lavage may provide stomach content data without the need to dissect the stomach out of fish.
I was able to discriminate between vegetated and non-vegetated sites based on number of the six main prey items present at each site. This would initially appear to suggest that there is the potential for perch to be limited by prey availability between the two habitat types. However, examination of the discriminant roots for each prey type and the associated site loadings showed that although chironomids, amphipods, ephemeropterans (except *Hexagenia*), and trichopterans were positively associated with vegetated sites, *Hexagenia*, nematodes, and oligochaetes were positively associated with non-vegetated sites. The fact that yellow perch included all of these organisms in their diet suggests that, although the invertebrate prey community was different between sites, perch were able to compensate by simply switching to alternate, more abundant prey types.

**Fish**

**Catch-Per-Unit-Effort (CPUE)**

Mid August CPUE data suggested that perch densities were far greater in the vegetated sites, compared with non-vegetated sites. However, CPUE for late August and September indicated that the densities of fish between the two sites was fairly equal with Mitchell’s Bay and Radio Tower sites having slightly higher fish densities. This result could indicate that the smaller fish present during the July sample might have been actively selecting the vegetated sites. Previous work by Weaver *et al.* (1997) noted that yellow perch showed increased abundance and dominance where vegetation was abundant, species rich, and structurally complex. Also several studies have shown that the congener Eurasian perch preferentially chose vegetated over non-vegetated habitats (Wang and Eckmann, 1994; Rossier *et al.*, 1996). However, other studies have shown no relationship between perch abundance and aquatic macrophytes. For instance, Fisher *et al.* (1999) found no influence of submerged vegetation on juvenile yellow perch abundance in two South Dakota lakes. It
appears that at least in the areas studied here, vegetated habitats may be most important for nursery areas, with fish possibly migrating to other areas of the lake after a certain size is reached. The fact that the Lakeview site seemed to have consistently fewer fish than the other two vegetated sites, may be a reflection of the composition of the macrophyte community. Weaver et al. (1997) found that yellow perch were more dominant and abundant in areas where vegetation was species rich and structurally complex as well as abundant. Lakeview vegetation was comprised mostly of Chara species with some larger more complex plants, but in general it was much less structurally complex and had a lower percentage of plant cover than either Mitchell’s Bay or Radio Tower.

**Growth**

The highly significant regression of fork length on otolith radius seen in this study supports the finding from Chapter 2 that otoliths are a useful tool in determining growth rates of YOY yellow perch. In addition this regression is identical to the one calculated for experimental fish. This also suggests that otoliths provide useful information on growth of YOY yellow perch, both in the lab and in the field. These results also agree with results of other researchers who have shown strong correlation between otolith radius and yellow perch length (e.g., Post and Prankevicius, 1987; Powles and Warlen, 1988). Although a second order polynomial regression was significantly better at describing the relationship between fork length and otolith radius, it severely underestimated growth of small fish (< 50 mm).

It is likely that the true relationship between otolith radius and fish length was allometric in yellow perch; however, an isometric relationship best described the biological relationship over the size range of fish looked at in this study. Otolith measurements extending to the larval phase would undoubtedly strengthen the relationship.
Separate regression of fork length on otolith radius of fish previously identified as belonging to a late-hatched cohort (Fitzgerald et al. In press) suggests that the late hatched fish may have a significantly different otolith-somatic growth relationship than early-hatched fish. If late-hatched fish experienced conditions that induced severe stress and reduction in growth, I would expect to observe a similar decrease in the slope of the relationship. Thus, fish of a specific size that were experiencing drastically reduced somatic growth would have larger otoliths than fish experiencing more favourable conditions. Such discrepancies between otolith and somatic size of fish undergoing severe stress have been observed in species as varied as striped bass (Secor and Dean, 1989), bloater (Rice et al., 1985), and guppies (Reznick et al., 1989). However, the difference in the otolith-somatic relationship seen in this study may be an artefact of the fact that the late hatched cohort comprised fish of only a very narrow size range (50-66 mm). When the regression for late-hatched fish was compared to the regression of early-hatched fish of a similar size range, there was no significant difference between the two relationships. Further age analysis on remaining fish would better elucidate the otolith-somatic growth relationship for both early and late hatched fish.

There was no significant difference in the growth of fish from vegetated and non-vegetated sites during the first two sample dates. Although there was a significant difference in mean size of fish taken from several of the sites, this difference in size was not reflected by corresponding differences in growth rates among sites. Once corrected for the size of the fish, growth rates were similar for all sites during July and mid-August samples. This result was not completely unexpected, since most fish were feeding on similar food items during at least the first sample period. Thus, vegetation state of habitat does not appear to influence early season growth of YOY yellow perch.
The smaller size of fish from the Mitchell’s Bay site may reflect this area’s importance as a nursery area for yellow perch (Goodyear et al., 1986). It is possible that nursery areas such as Mitchell’s Bay act somewhat like staging grounds for newly settled fish. Such areas may see continued influxes of small fish representing progressively later hatch dates. Fish already resident in these nursery areas may migrate once they reach a certain size, which probably corresponds to completion of their ontogenetic diet shift. This diet shift may then enable them to migrate to other habitats and utilise a wide variety of prey types.

Although YOY perch do go through one ontogenetic migration early in their life, it is usually a migration from the pelagic zone to the littoral zone once the fish reach a size of approximately 30mm (Post and McQueen, 1988). This migration is concomitant to ontogenetic changes in diet and visual acuity (Wahl, et al. 1993). Density dependent processes could mediate a further migration away from a nursery or staging area if the area continued to receive influxes of new recruits. This would be especially true if the area also received recruits of other, potential competitor species. Post et al. (1995) provide evidence for such density dependent migrations (or cohort splitting) in YOY yellow perch from Lake St. George, Ontario. They observed that the perch migrating away from the vegetated littoral zone consistently had lower growth rates compared to the fish remaining in the littoral zone.

This is essentially the opposite of the result seen in this study. Fish in the vegetated sites of Mitchell’s Bay and Radio Tower showed significantly lower growth rates during the late August and late September sampling periods. This result was the opposite of what I expected to observe. There are two probable factors that likely act in conjunction to produce the effect of small fish size and decreased growth in Mitchell’s Bay and Radio Tower sites compared to non-vegetated sites.
The first factor may explain why yellow perch in non-vegetated habitats showed similar growth to fish in vegetated habitats (opposite to what was expected). It has been shown in previous studies that the presence of zebra mussels can significantly alter the benthic environment when they are present. The increased abundance of zebra mussels in non-vegetated areas of Lake St. Clair and associated increased abundance of some benthic organisms (oligochaetes, nematodes, and amphipods) is similar to what was noted by Griffiths (1993) for Lake St. Clair. The fact that yellow perch included all of these organisms in their diet suggests that zebra mussels may actually increase the number of prey items available for yellow perch in non-vegetated habitats. Thayer et al. (1997) were able to show that presence of zebra mussels in enclosures actually enriched the sediment and increased habitat complexity causing increases in both oligochaetes and crustaceans. They were then able to link this increase in the benthic prey community to increases in year 2+ perch growth.

Although year 2+ fish would obviously feed on larger benthic organisms than the 0+ fish examined in this study, the same trend may be occurring. Thus, perch migrating away from historical nursery areas in Lake St. Clair may actually encounter more favourable environments compared to pre-zebra mussel introduction and compared to high-density nursery areas. In addition, predation pressure probably varies with respect to vegetated and non-vegetated habitats. Future studies into predation pressure between habitats would further our understanding of the biotic factors influencing juvenile perch growth in each habitat.

Similar CPUE values for yellow perch in both non-vegetated and vegetated sites during the later two dates would seem to contradict the assumption that Mitchell’s Bay and Radio Tower are high density nursery areas. However, this low CPUE could simply be the
result of more fish moving to new areas or it could also reflect higher predation pressure in vegetated sites. In addition, yellow perch are only one of the several species known to use this area as a nursery (Goodyear et al., 1982). Thus the similar CPUE for perch would not reflect an increase in interspecific competition in vegetated areas. Although this explanation may account for the lack of an expected decreased growth rate associated with fish in non-vegetated sites, it does not explain why fish in the two vegetated sites had much lower growth rates than those in non-vegetated sites.

The second factor possibly leading to the observed growth rates also lends support to the idea that Mitchell’s Bay, and to a lesser extent the Radio Tower site, may be an important nursery or staging area for young yellow perch. The majority of the fish identified as belonging to the late-hatched cohort were captured at these sites with very few of the larger early-hatched fish occurring in these sites. These larger, early-hatched fish were captured in the non-vegetated sites and the Lakeview site, which suggests that they are migrating, as opposed to experiencing high mortality through predation. For example, fish collected at the nearshore Mitchell’s Bay site during this August 1998 were predominantly (>90%) small, late-hatched fish with a primary mode c. 65 mm. However, fork length of fish captured offshore (<3m depth) of the Mitchell’s Bay site ranged from 61 to 109mm with a mode c. 80 mm. and consisted predominantly of early-hatched fish (Fitzgerald et al. In Press). It is possible that the fish present in these two vegetated sites consisted of progressively later hatched fish throughout the year, and that these late-hatched fish had experienced sub-optimal growth conditions in terms of critical zooplankton food availability or water temperatures (Magnusson et al., 1979; Shuter and Post, 1990; Kamler, 1992). The fact that late-hatched fish appeared to have a significantly different otolith-somatic growth relationship, lends support to this explanation since it has been shown that such sub-optimal
conditions can lead to a breakdown of this relationship (Secor and Dean, 1989). The fact that I did not capture any of the smaller late-hatched fish at any of my other sites, would explain why fish from those sites continued to display higher growth rates and mean sizes throughout the season, while growth rates of fish at the two vegetated sites was apparently reduced. This idea is supported by the fact that fish from the vegetated Lakeview site had similar size and growth rates to the fish in all non-vegetated sites throughout the sampling season.
Table 3.1. Water temperatures for each sampling site at each sampling period.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Water Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio Tower</td>
<td>03-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Mitchell's Bay</td>
<td>03-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Lakeview</td>
<td>08-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Maidstone</td>
<td>08-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Belle R.</td>
<td>09-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Stoney Pt.</td>
<td>09-Jul-98</td>
<td>22</td>
</tr>
<tr>
<td>Radio tower</td>
<td>13-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Mitchell's Bay</td>
<td>13-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Belle R.</td>
<td>14-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Stoney Pt.</td>
<td>14-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Lakeview</td>
<td>15-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Maidstone</td>
<td>15-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Stoney Pt.</td>
<td>27-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Radio Tower</td>
<td>27-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Mitchell's Bay</td>
<td>27-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Lakeview</td>
<td>28-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Maidstone</td>
<td>28-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Belle R.</td>
<td>28-Aug-98</td>
<td>23</td>
</tr>
<tr>
<td>Maidstone</td>
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<tr>
<td>Belle R.</td>
<td>24-Sep-98</td>
<td>19</td>
</tr>
<tr>
<td>Radio Tower</td>
<td>28-Sep-98</td>
<td>18</td>
</tr>
<tr>
<td>Mitchell's Bay</td>
<td>28-Sep-98</td>
<td>18</td>
</tr>
<tr>
<td>Lakeview</td>
<td>12-Oct-98</td>
<td>16</td>
</tr>
<tr>
<td>Stoney Pt.</td>
<td>12-Oct-98</td>
<td>16</td>
</tr>
</tbody>
</table>
Table 3.2. Results of Discriminant function analysis predicting vegetated or non-vegetated membership from benthic organism abundance. There is only one discriminant root as sites were pooled to provide adequate number of cases.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Canonical r</td>
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<td>.977</td>
<td>.966</td>
<td>.982</td>
</tr>
<tr>
<td>Overall p-value</td>
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<td>&lt;.001</td>
<td>&lt;.001</td>
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<tr>
<td>Wilks Lambda</td>
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<td>.045</td>
<td>.065</td>
<td>.035</td>
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<tr>
<td>Invertebrate</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Factors</td>
<td>Loadings</td>
<td>Loadings</td>
<td>Loadings</td>
<td>Loadings</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>-.450</td>
<td>-.664</td>
<td>-1.297</td>
<td>.927</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>-.669</td>
<td>-.444</td>
<td>-.542</td>
<td>.136</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>-.338</td>
<td>-.817</td>
<td>.228</td>
<td>-.103</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>-.457</td>
<td>-.390</td>
<td>-.282</td>
<td>.270</td>
</tr>
<tr>
<td>Hexagenia</td>
<td>.043</td>
<td>.284</td>
<td>.494</td>
<td>-.164</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>.152</td>
<td>.492</td>
<td>-.858</td>
<td>-.107</td>
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</tbody>
</table>
Table 3.3. Table of reduction in sum of squares tested against the mean square remaining after curvilinear regression showing significance of departure from linear regression.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Sum of Squares (SS)</th>
<th>Mean Square (MS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deviations from</td>
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<td>5588.19</td>
<td></td>
</tr>
<tr>
<td>linear regression</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deviations from</td>
<td>395</td>
<td>4379.39</td>
<td>11.087</td>
</tr>
<tr>
<td>curved regression</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduction in SS</td>
<td>1</td>
<td>1208.81</td>
<td>1208.81</td>
</tr>
<tr>
<td>F-value</td>
<td></td>
<td></td>
<td>109.01</td>
</tr>
<tr>
<td>p-value</td>
<td></td>
<td></td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 3.1. Map of Lake St. Clair showing location of vegetated (dark circles) and non-vegetated (white circles) sampling sites encompassing the south-eastern shoreline.
Figure 3.2. Mean numbers of benthic organisms collected by Petit Ponar grab at vegetated and non-vegetated sites in Lake St. Clair during a) July 3-9, and b) Aug 13-15, 1998.
Figure 3.3. Mean numbers of benthic organisms collected by Petit Poner grab at vegetated and non-vegetated sites in Lake St. Clair during a) Aug 27-28, and b) Sept 24-Oct 12, 1998.
Figure 3.4.  a) Mean (+standard error) Catch-Per-Unit-Effort (CPUE) and b) CPUE for each site for YOY yellow perch caught in fine mesh gill nets in vegetated and non-vegetated habitats for the last three sampling dates during 1998.

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**Figure 3.5.** Proportions of organisms identified in the diet of yellow perch caught in vegetated and non-vegetated habitats for a) July 3-9, and b) Aug 13-15, 1998.
Figure 3.6. Proportions of organisms identified in the diet of yellow perch caught in vegetated and non-vegetated habitats for a) Aug 27-28, and b) Sep 24 – Oct 12, 1998.
Figure 3.7. Chesson’s alpha index each organism in yellow perch from vegetated and non-vegetated habitats, during a) Aug 13-15, b) Aug 27-28, and c) Sept 24-Oct 12.
Figure 3.8. Regression of Fork Length (mm) on otolith radius (μm) for yellow perch from Lake St. Clair (early and late hatch) and experimental fish used in growth studies. Model for all wild fish is $FL = (179.07)* (OR) - 19.83$, $r^2 = 0.95$, $n = 398$. 
Figure 3.9. Regression of mean daily growth (mm/day) on fork length (mm) for yellow perch from Lake St. Clair, 1998. Model is $GR = (-0.005) * (FL) + 0.861$, $r^2 = 0.16$, $n = 277$. 
Figure 3.10. a) Mean (± standard error) fork length (mm) and b) standardised mean daily growth rate (mm/day) of yellow perch captured at each site in Lake St. Clair during July 3-9, 1998.
Figure 3.11. a) Mean (± standard error) fork length (mm) and b) standardised mean daily growth rate (mm/day) of yellow perch captured at each site in Lake St. Clair during August 13-15, 1998.
Figure 3.12. a) Mean (± standard error) fork length (mm) and b) standardised mean daily growth rate (mm/day) of yellow perch captured at each site in Lake St. Clair during August 27-28, 1998.
Figure 3.13. a) Mean (± standard error) fork length (mm) and b) standardised mean daily growth rate (mm/day) of yellow perch captured at each site in Lake St. Clair during September 24-October 12, 1998.
GENERAL CONCLUSIONS

In conclusion it is apparent that the analysis of otolith microstructure is a useful tool in determining growth and age of juvenile yellow perch. Temperature had a significant effect on growth and tended to mask differential effects of ration on growth of lab reared fish. This highlighted the need for field studies to account for temperature in the experimental design in order to eliminate possible confounding effects due to temperature discrepancies between experimental units.

The otolith-somatic growth relationship in juvenile yellow perch appeared fairly stable across a wide range of fish sizes and growth regimes; however, care should be taken not to extrapolate growth values beyond the size range or growth regimes depicted by any particular sample of fish. The fact that late hatched fish in Lake St. Clair had a significantly different otolith-somatic growth relationship than early-hatched fish, may indicate that the late-hatched fish experienced sub-optimal conditions during their early life history.

Estimated growth from otolith analysis was able to predict actual changes in growth of lab-reared yellow perch brought about by short-term changes in both ration and temperature. Thus, I was able to apply this technique to natural populations and try to link diet and growth of juvenile yellow perch between vegetated and non-vegetated habitats. However, there was a time lag between when changes due to ration were apparent and when they were first statistically detectable. These changes in otolith increment widths were most apparent when increment widths were averaged over a 5-10 day period. Thus, I used the last 10 otolith increments to provide an average growth rate of yellow perch from vegetated and non-vegetated habitats in Lake St. Clair. This incorporated a long enough time span to detect differences in growth, while still ensuring that the fish was present in the respective habitat for the duration of the period.
In general it appears that the ongoing shift in Lake St. Clair from a phytoplankton-dominated turbid state to a clearer macrophyte-dominated state may benefit production of yellow perch, although in somewhat unexpected ways. It was hypothesised that perch would benefit from the increased benthic invertebrate production associated with increased macrophytes in vegetated areas. Although this may in fact be occurring, the increased benthic invertebrate production associated with increased zebra mussels colonisation in non-vegetated areas also appears to benefit juvenile yellow perch. Although there were distinct differences in the prey community and diet of yellow perch between vegetated and non-vegetated habitats, there did not appear to be a significant difference in growth rates of YOY yellow perch related to habitat type.

This result was contrary to the expected result, i.e., that increased abundance and diversity of benthic invertebrates in vegetated sites would lead to increased growth of YOY yellow perch in vegetated habitats. However, the presence of zebra mussels and the concomitant increase in abundance of associated benthic invertebrates in non-vegetated areas probably increased the prey base in non-vegetated habitats relative to pre-zebra mussel conditions. Although these benthic prey are composed of a different mix of organisms, the broad, opportunistic, feeding behaviour seen in YOY yellow perch may compensate for changes in prey types.

The lower growth rates observed in fish from Mitchell’s Bay and Radio Tower sites during the later part of the season are likely related to the progressively later hatch dates of these fish, as opposed to habitat type. It is likely that later hatched fish experienced sub-optimal growth conditions in terms of temperature and co-ordination with important zooplankton prey communities which lead to decreased size and growth of this late-hatched cohort.
LITERATURE CITED


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### APPENDIX 1

Table of macrophyte species present, species coverage (%), and total coverage (%) for vegetated and non-vegetated sites sampled in Lake St. Clair, 1998.

<table>
<thead>
<tr>
<th>Site and species present</th>
<th>Species coverage (%)</th>
<th>Total coverage (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maidstone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chara spp.</td>
<td>= 4</td>
<td></td>
</tr>
<tr>
<td><em>Myriophyllum spicatum</em></td>
<td>= 1</td>
<td></td>
</tr>
<tr>
<td>Belle R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chara spp.</td>
<td>= 5</td>
<td></td>
</tr>
<tr>
<td>Stoney Pt.</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Lakeview</td>
<td>= 70</td>
<td></td>
</tr>
<tr>
<td><em>Najas flexilis</em></td>
<td>= 10</td>
<td></td>
</tr>
<tr>
<td><em>Potamogeton richardsonii</em></td>
<td>= 10</td>
<td></td>
</tr>
<tr>
<td><em>Potamogeton spp. (narrow)</em></td>
<td>= 5</td>
<td></td>
</tr>
<tr>
<td><em>Vallisneria americana</em></td>
<td>= 15</td>
<td></td>
</tr>
<tr>
<td><em>Myriophyllum spicatum</em></td>
<td>= 10</td>
<td></td>
</tr>
<tr>
<td>Chara spp.</td>
<td>= 15</td>
<td></td>
</tr>
<tr>
<td><em>Elodea canadensis</em></td>
<td>= 5</td>
<td></td>
</tr>
<tr>
<td>Radio Tower</td>
<td></td>
<td>= 90</td>
</tr>
<tr>
<td><em>Najas flexilis</em></td>
<td>= 15</td>
<td></td>
</tr>
<tr>
<td><em>Potamogeton richardsonii</em></td>
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<td><em>Potamogeton spp. (narrow)</em></td>
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<td><em>Elodea canadensis</em></td>
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VITA AUCTORIS

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Date of Birth: April 16, 1967

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