THE IMPORTANCE OF BIOTIC FACTORS AND GROWTH IN THE RECRUITMENT

OF YOUNG-OF-THE-YEAR WALLEYE (*Stizostedion vitreum*)

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ABSTRACT

The Importance of Biotic Factors in the Recruitment of Young-of-the-Year Walleye

(*Stizostedion vitreum*)

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In this dissertation, I investigated the importance of post-larval size-mediated interactions on walleye recruitment. Survival in young fishes is often size-specific, with larger individuals surviving better than smaller individuals. Thus, increasing growth rates is believed to afford a survival advantage, particularly during a number of critical post-larval periods. My research investigated the importance of increasing body size on predator-prey associations, habitat selection, overwinter survival and body composition of young-of-year (YOY) walleye. This research demonstrated that the life history strategy of post-larval YOY walleye followed the predictions of the size-selective survival hypothesis for a brief period (approximately 1 month post-larval) by residing in areas of high prey density and growing rapidly. After this period, there was very little support for the size-selective hypothesis, as only limited evidence for size-selective overwinter survival in YOY walleye was found in either pond or lake experiments. Predators were thought to play an important role in mediating growth rates by influencing both early and late summer habitat selection, and predators strongly influenced the body composition of YOY walleye during overwinter experiments. Predators are typically the mechanism behind size-selective mortality in aquatic systems, but predator-induced size-selective mortality can be mediated by changes in habitat selection and behaviour. Thus, this dissertation found only limited evidence to support the contention that size-specific mortality influenced recruitment variability in post-larval YOY walleye.

PREFACE

Chapters 2 and 3 of this dissertation have been submitted to Archive für

Hydrobiologie and Canadian Journal of Fisheries and Aquatic Sciences, respectively,

with Michael G. Fox as the co-author. My role in the development of the papers included

the experimental design, data collection, data analysis, and drafting of the papers, while

Michael's role included collaborating on experimental design, advice on data analysis,

and editing the draft papers.

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TABLE OF CONTENTS

Chapter 4. The Influence of Predation Risk on the Overwinter Mortality and Energetic

Relationships of Young-of-the-Year Walleye (*Stizostedion vitreum*)

Chapter 5. The Relative Contribution and Survival of Two Stocked Walleye Fingerling

Sizes in Six Eastern Ontario Lakes

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1.

General Introduction

Understanding the variability inherent in recruitment remains the biggest challenge for ecologists studying fish population dynamics (Sissenwine 1984). Ecologists consider a fish to be recruited if it survives long enough to reproduce, although fishery managers use a slightly different definition and consider recruitment to encompass any fish capable of capture by the fishery regardless of reproductive status (Helfman et al. 1997). The relative success of year-classes fluctuates widely, and this variability is often unrelated to the number of spawning adults, suggesting that other factors play an important role in the survival of young fishes (Wootton 1990). The highest variability in mortality during the early life history of fishes is typically not related to variation in egg production, but rather to the rate of survival in the larval life stage (Hjort 1914). Larval survival in fishes can vary tenfold or greater among years, and survival is believed to depend upon food availability, predator densities, and a suite of potentially deleterious physical conditions, including water temperature, water levels, and spring wind patterns (Houde 1987, Claramunt and Wahl 2000). Variable mortality is not only a characteristic of the larval life stage, though, as mortality continues to be high and variable throughout the earliest life stages (Houde 1987). Research on some species has shown recruitment variability to be highest in the juvenile, as opposed to larval, stage (Cushing 1974, Forney 1976, Houde 1987). This suggests that, while the larval stage remains an important source of mortality for all fish species, some species must survive a number of critical periods before the strength of a given year-class is determined.

High mortality during the early life history of fishes ensures that the probability of an individual surviving to recruitment are low. As such, much effort has been spent in determining whether the survival of individual fish appears to be a random event, or whether there appears to be certain behavioural, physiological, or morphological characteristics that enhance the probability of survival (Crowder et al. 1992). One such

1

characteristic that has received a great deal of attention is the importance of body size in the early survival of fishes (Sogard 1997). Subtle changes in growth can influence the mortality of fishes during the larval and juvenile stages, as mortality rates typically decrease with increasing body size (Peterson and Wroblewski 1984, Houde 1987). This means faster growing individuals spend less time in vulnerable size-classes, and ultimately may even reach a size-based refuge (Houde 1987). Survival during these early life stages is thought to be strongly size-dependent, as size-selective predation (Post and Evans 1989a, 1989b) and size-selective starvation (Miller et al. 1988) affect mortality. Increasing growth rates during the early life stages can reduce mortality, and ultimately increase year-class strength (Rice et al. 1993). Therefore, research into factors that influence the size-dependent growth and survival of young fishes may improve our understanding of recruitment variability, which continues to be a worldwide issue of ecological and economic importance.

One species where the uncertainties surrounding recruitment remain in the forefront despite years of research is the walleye (*Stizostedion vitreum*), which is the basis of important sport and commercial fisheries across North America. Like most fishes, walleye have periodic strong year-classes, often followed by years of negligible recruitment. Attempts to understand the factors behind these variable recruitment events have revealed many interesting ecological and environmental phenomena involved in walleye population dynamics, and a number of processes have been identified as potential limiting factors in the early life history of walleye, including unfavourable environmental conditions and complex predator-prey dynamics (Johnson et al. 1996). Walleye is one species where mortality appears to primarily be regulated during post-larval stages, as post-larval mortality increased the variation in year-class size and obscured initial differences in larval abundance across eight year-classes in Oneida Lake (Forney 1976). However, on the whole, our understanding of the ecological mechanisms behind recruitment variability in walleye remains poor (Johnson et al. 1996).

2

Like most percids, walleye are spring broadcast spawners, releasing eggs and sperm over shallow cobble areas when water temperatures are about 7 - 9 °C (Scott and Crossman 1973). Depending on water temperature, eggs hatch in approximately three weeks, and within three-to-five days, 6-9 mm larval walleye begin foraging for zooplankton in the pelagic zone (Houde and Forney 1970). After approximately one month, when larval walleye reach 25-50 mm, they turn piscivorous and become demersal (Raney and Lachner 1942, Forney 1976). Young-of-year (YOY) walleye then grow relatively quickly, reaching upwards of 200 mm by the end of their first growing season (Scott and Crossman 1973).

A number of abiotic and biotic factors have been found to influence walleye survival during the earliest life stages. Important abiotic factors include water level or flow, wind, and the rate of spring water warming, while important biotic factors include size of spawning stock, prey availability, cannibalism, and predation (Forney 1976, Koonce et al. 1977, Kallemeyn 1987, Johnston et al. 1995, Madenjian et al. 1996, Leis and Fox 1996, Hansen et al. 1998). In general, abiotic factors are thought to more strongly affect egg and larval survival, while post-larval life stages are believed to be more influenced by biotic factors. Modeling has shown that a combination of abiotic and biotic factors are necessary to explain observed variable recruitment patterns (Koonce et al. 1977, Madenjian et al. 1996, Hansen et al. 1998). The synchrony of strong year-classes across geographic areas suggests that climatic variables are probably important across broad spatial scales, while biotic factors may be more important at a local level.

The mechanisms behind the effects of biotic factors on walleye recruitment are not as well understood. Changes in YOY walleye abundance between the pelagic and demersal stage, within the demersal stage, and during the first over-winter period suggest that those three stages represent potential life stage bottlenecks (Forney 1976). Mortality after the first overwinter period is low, suggesting that fish surviving past this period would be successfully recruited to the adult population (Forney 1976). Size-mediated

3

interactions between YOY walleye, their prey, and potential predators are likely behind the inconsistent role played by biotic interactions. Forney (1976) suggested that the strength of other YOY year-classes, in particular yellow perch (*Perca flavescens*), is critical to the successful transition from pelagic (zooplanktivorous) to demersal (piscivorous) stage, as large numbers of YOY perch could reduce the effect of cannibalism, by providing alternate prey. In addition, YOY yellow perch are an important food item in the diet of YOY walleye (Raney and Lachner 1942), and are likely important in the switch to piscivory. The availability of prey, and the resulting increase in walleye energy levels, are also important in determining whether female walleye will spawn in Lake Erie (Madenjian et al. 1996), and may be important in explaining the distribution of YOY walleye in river systems (Leis and Fox 1996).

Limited research into the importance of body size on the post-larval survival of walleye suggests that there is significant size variation within walleye populations (Carlander 1997) and that mortality can be size-dependent (Chevalier 1973, Forney 1976, Madenjian et al. 1991), thereby providing the conditions necessary for the occurrence of size-selective mortality (Sogard 1997). Increased body size not only improves survival by allowing individuals to outgrow the gape of potential predators, it increases the number and size of potential prey items and improves intra-cohort competitive abilities (Sogard 1997). These factors can lead to positive feedbacks that can further enhance growth differences among individuals. For piscivores, slight alterations in the onset of piscivory can lead to dramatic differences in size variation within a cohort (Pine III et al. 2000). The onset of piscivory is quite variable among and within walleye populations (Carlander 1997), further emphasizing the potential for intra-population size differences. Given the potential for size variability within walleye cohorts and the importance of biotic factors on juvenile walleye survival, it is possible that size-selective factors may influence the variable survival patterns observed during post-larval walleye life stages.

4

Walleye are often stocked when natural recruitment is deemed unsuitable. The goals of stocking are often poorly defined, and stocking events are rarely assessed (Ellison and Franzin 1992), so determining the success or failure of the stocking is typically difficult. In general, walleye stocking has been unsuccessful, particularly when stocking occurs in waterbodies containing pre-existing populations (Laarman 1978, Ellison and Franzin 1992). Stocking walleye into existing populations can reduce growth rates and affect the year-class strength of associated year-classes (Li et al. 1996a, Li et al. 1996b), so increases in abundance due to stocking are rarely realized (Fluri 1996, Li et al. 1996b).

The stocking of walleye into waterbodies with existing populations may allow tests of the size-selective mortality paradigm to be undertaken. Researchers interested in addressing size-dependent mortality have used hatchery-reared individuals in a number of investigations; in general, results support the contention that larger individuals have reduced mortality rates (Wahl and Stein 1989, Pope et al. 1997, McKeown et al. 1999). Walleye in particular may be good candidates for such studies because rearing procedures typically lead to the production of individuals from hatcheries that are smaller than those found concurrently in native populations, although hatcheries attempt to keep size variation within hatchery cohorts small to reduce the potential of cannibalism.

As much attention has been focused on recruiting walleye to the adult stage in order to enhance important fisheries, relatively little research has addressed the behaviour of young walleye. Recent laboratory studies by Wahl (1995), Wahl et al. (1995), Einfalt and Wahl (1997), and Jonas and Wahl (1998) have revealed new insights in the areas of YOY walleye foraging, habitat selection, and anti-predator behaviour that appear to support the contention of Forney (1976) that walleye face a number of critical periods during their early life history. However, our knowledge of the early life history of walleye remains incomplete, and the relationship between early growth, ontogenetic shifts, and survival has not been adequately addressed.

5

The goal of my dissertation is to address one potential aspect of walleye recruitment variability by investigating the importance of size-mediated interactions on survival to age 1. As walleye survival is most variable between the post-larval and first overwinter periods (Forney 1976), research focusing on size-based ecological processes during this period should help our understanding of walleye recruitment dynamics. The following paragraphs will briefly introduce the four research chapters that comprise the balance of the thesis, and highlight the hypotheses and predictions tested therein. A general discussion, focusing on the role of size-mediated interactions in YOY walleye, will be the sixth and final research chapter.

In chapter two, I explore the role of sampling technique and level of numerical resolution on data collected from the same fish community. This chapter developed from my first attempt at investigating the habitat and species associations of YOY walleye (chapter three), using two sampling techniques (experimental smallmesh gillnets and underwater visual transects) typically employed in the sampling of fishes not readily captured by seining littoral areas. While both techniques were able to sample a variety of species, neither was able to sample YOY walleye consistently. Nonetheless, the collected data could be used to compare the relative sampling ability of the two techniques, and make recommendations for the best technique to use in the following sampling year given the hypotheses of interest.

Research comparing fish sampling techniques is relatively uncommon, which is surprising given the fact that the species collected by various sampling techniques can vary widely (Hayes et al. 1996). Despite the fact that both smallmesh gillnets and visual transects are commonly used to sample small fishes, I hypothesized that the two techniques would sample different fish species, and given that underwater visual methods tend to sample more species than other methods (Goldstein 1978, Rossier 1997), predicted that underwater visual transects would sample more species than gillnetting. As different species inhabit different areas of the littoral zone, I also hypothesized that

the differences between these techniques would not be consistent between structurally complex and open habitats. Finally, as the ultimate goal of chapter two was to suggest the best technique for the following study season, I undertook a comparison of the techniques' ability to sample both potential predator and prey fishes.

The third chapter focused specifically on the *in situ* size-mediated interactions of YOY walleye in a mid-sized mesotrophic lake. YOY walleye become demersal and piscivorous in early summer (Houde and Forney 1970), but there is little consensus as to their habitat use or species associations throughout their first year. Habitat selection is an important component of anti-predator behaviour, and can mitigate size-selective predation pressure and affect growth rates (Werner et al. 1983b, Gotceitas and Colgan 1990). Leis and Fox (1996) found no strong YOY walleye habitat associations, and suggested that young walleye were distributed primarily in areas of high prey densities. Inhabiting areas where prey densities are highest could increase juvenile walleye foraging rates, reducing the length of time walleye are vulnerable to predators. Therefore, investigating the habitat and species associations of YOY walleye may be important in understanding why walleye mortality patterns are so variable during their first summer. As the study required the sampling of YOY walleye and their potential predators and prey, an underwater visual technique was selected to allow the maximum number of species to be sampled across a variety of littoral zone habitats. I then tested the following hypotheses about the distribution of YOY walleye during the demersal phase of their early life history: (1) YOY walleye will be habitat generalists, except to avoid high cover habitats dominated by aquatic macrophytes; (2) The distribution of YOY walleye will be positively related to that of their prey; and (3) The distribution of YOY walleye will be negatively related to that of their predators.

In the fourth chapter, I investigate the role of body size and predation risk on over-winter survival in a YOY walleye cohort. Size-dependent over-winter mortality, where mortality is relatively higher for smaller fish, is commonly observed in temperate

freshwater fishes (e.g. Toneys and Coble 1979, Post and Evans 1989a), including walleye

(Chevalier 1973). This period is thought to be extremely important in ultimate formation

of walleye year-classes in some lakes (Forney 1976), and is therefore a time when size-

selective mortality could potentially affect walleye recruitment. Explanations for this

phenomenon include differences in size-specific metabolic costs (Paloheimo and Dickie

1966), size-specific predation (Post and Evans 1989a), or a combination of both

explanations (Miranda and Hubbard 1994a). By rearing individually marked YOY

walleye over-winter in outdoor nursery ponds, I tested the following predictions; that

smaller individuals of a YOY walleye cohort would have lower pre-winter energy levels,

and deplete them at a higher rate than larger individuals; that no differences in over-

winter survival among the individuals of a walleye cohort were expected in predator-free

ponds, as YOY walleye are able to forage during the over-winter period; that for YOY

walleye reared over-winter with predators, physiological stress combined with size-

selective predation on the smaller individuals, would lead to size-specific over-winter

mortality.

In the final research chapter, I investigated the outcome of a walleye fingerling

'paired-plant' experiment in six eastern Ontario inland lakes. The stocking of walleye to

supplement or rehabilitate stocks that are no longer able to sustain themselves has

become quite common throughout North America, though relatively little effort has gone

into investigating the success or failure of these stocking events (Laarman 1978, Ellison

and Franzin 1992). Walleye can be stocked at a variety of times and life stages, with the

resulting fish facing potentially different ecological and physiological conditions than can

ultimately affect survival. In this experiment, walleye fingerlings were stocked in both

the early summer and late fall six study lakes (four lakes were stocked by the Ontario

Ministry of Natural Resources in 1992 and 1993, while two additional lakes were stocked

in 1998). As the potential for size differences existed between the two fingerling types,

the resulting survival patterns were examined across lakes and years to determine the

extent to which body size may have influenced the observed patterns. Walleye stocked in the fall were likely smaller at that time than those that had been stocked in the summer, and the resulting interactions could have led to competition and predation asymmetries (Persson 1988), ultimately allowing the importance of size-mediated interactions (in this case, of whether size-selective mortality occurs in walleye during their first summer) to be assessed. As such, the objective of this chapter was to investigate growth patterns, the relative contribution, and the relative survival rate of stocked summer and fall walleye fingerlings to the adult population. I hypothesized that there would be survival differences between the fingerling types due to differences in initial body size, and predicted that because of these size differences summer fingerlings will have greater survival than fall fingerlings.

The importance of size-specific mortality, and consequently body size, on recruitment has been demonstrated in many, but not all, fishes (review by Sogard 1997). By investigating the importance of size-mediated interactions throughout the period identified by Forney (1976) as the time when walleye mortality was most variable, I hope to address the role of body size in the survival of YOY walleye, ultimately relating the importance of ecological factors such as habitat selection, prey availability, and predation pressure to the recruitment variability inherent in walleye populations.

Chapter 2.

Comparison of two methods for sampling a littoral zone fish community

2.1. Introduction

Determining a single, effective method of sampling fish communities is nearly impossible. Because of variation in fish body shape, size and behaviour, researchers have had to develop many different sampling strategies. Standard fisheries assessment techniques fall into two broad sampling types, active and passive capture techniques, though a variety of underwater visual assessment methods have also been developed (Helfman 1983). However, all available techniques are biased towards certain species, sizes, or body shapes (Hayes 1983, Hubert 1983), and some are harmful to either the fish or the aquatic habitat in general (Serafy et al. 1988).

In some cases, interest in community-level factors such as predator and prey abundance requires researchers to use the sampling technique likely to lead to the most complete fish community survey. For example, habitat selection in juvenile fishes can depend on factors such as predation risk and prey availability (Werner et al. 1983b, Rozas and Odum 1988), and growth rates can be reduced when juvenile fishes trade-off higher prey availability for safer habitats (Mittelbach 1981, Werner and Gilliam 1984, Abrahams and Dill 1989). As mortality rates decrease with increasing body size (Houde 1987, Miller et al. 1988), habitat choices may cause juvenile fishes to remain in vulnerable size-classes for longer periods, ultimately influencing their recruitment to the adult population. Therefore, some studies require a technique (or multiple techniques)

capable of sampling across the spectrum of fish communities in order to determine the importance of predators and prey on habitat selection.

The difficulty in effectively surveying an entire fish community becomes particularly obvious when attempting to sample fishes in the littoral zone. Heavy vegetation, submerged logs, and boulders make active capture techniques impossible to use in many areas (Hayes 1983), so despite their selective nature, gillnets are often used to sample littoral fish communities (Stang and Hubert 1984, Hubert and O'Shea 1992, Weaver et al. 1993, Rossier 1997). Experimental gillnets, where panels of different sized mesh are tied together, allow for a wide size-range of fishes to be sampled using a single net. As long as fish do not need to be captured, another type of technique capable of sampling a wide size-range of fishes is direct underwater observation. A number of visual transect and time-series techniques have been developed for snorkelers and divers (Keast and Harker 1977, Jones and Thompson 1978, Bohnsack and Bannerot 1986), though in comparison to marine studies, these techniques are rarely used in freshwater systems.

Both gillnets and direct underwater observations introduce unique sampling biases. Gillnets are size-selective and less efficient in sampling small fishes relative to larger ones because an individual fish's catchability decreases with decreasing mesh size (Hamley 1975). Direct underwater observations typically under-represent cryptic and pelagic species (Sale and Douglas 1981, Brock 1982), and introduce the potential for observer bias (Rossier 1997). In addition, the sampling ability of both techniques is influenced by factors such as water temperature, visibility, and light levels (Cui et al. 1991, Hillman et al. 1992, Hansson and Rudstam 1995). However, both techniques are

capable of sampling a diversity of fishes in complex habitats, and neither leads to permanent habitat damage (Hubert 1983, Helfman 1983).

Despite the potential limitations of most littoral zone sampling techniques, few studies have assessed the relative sampling ability of underwater visual techniques and more traditional sampling procedures. Differences have been found in abundance estimates between visual methods and other sampling techniques, with underwater observations tending to provide lower abundance estimates than more traditional techniques (Hickford and Schiel 1995, Thurow and Schill 1996, Connell et al. 1998). However, visual techniques have generally produced higher species counts (Goldstein 1978, Rossier 1997). None of these studies have compared visual assessments with other sampling techniques over a range of littoral zone habitats. Such a comparison would be useful, as it would enable fish ecologists to interpret the results of a particular sampling method in light of habitat-related bias.

The main objective of this study was to investigate a freshwater fish community using experimental gillnets and underwater visual transects, and determine which sampling technique more thoroughly assessed the available species by (1) comparing the numbers of species and relative species abundance obtained from underwater visual transects and gillnetting, and (2) determining whether any sampling differences between the two procedures are consistent across a variety of littoral zone habitats. Based on previous work published in this area, I predicted that underwater visual transects would produce more species than gillnetting, and therefore provide a more complete picture of the fish community. I also predicted that the differences between these techniques would not be consistent between structurally complex and open habitats.

2.2. Methods

Study Site

This study was performed on Big Clear Lake (44° 43' W, 76° 55' N), a 337 ha waterbody located near the town of Arden, Ontario, Canada. Big Clear Lake was selected for this research because habitat data were already available from an extensive walleye (*Stizostedion vitreum*) habitat use study (D. Seip, unpublished data). The surrounding basin is typical of the Precambrian Shield, with rock outcroppings and thin pockets of sandy soil. Big Clear Lake is a headwater lake fed by two major inflow streams, with a single drainage outlet. The lake itself consists of a number of large bays, roughly divided into four interconnected basins. Irregular glacial scouring has led to the formation of numerous small islands and shoals throughout the lake, resulting in a large and diverse littoral zone. The lake is relatively shallow (average depth = 6.6 m), and is thermally stratified from May to November. Water quality parameters for Big Clear Lake are typical of a mesotrophic waterbody in Canada (pH = 8.3, total dissolved solids = 145 mg/l, total phosphorus = 15μg/l (unpublished data, Ontario Ministry of the Environment, 1984). Surface water temperature ranged from 21 - 26°C over the duration of the study, while Secchi depths ranged from 3.6 - 4.1 m. The shoreline of Big Clear Lake is moderately developed, with permanent homes and cottages surrounding much of its perimeter.

Sampling Procedures

A total of 18 sites, representing six habitat types, were sampled using visual transects and a small-mesh gillnet (Figure 2.1). All sites had to contain a large enough patch of continuous habitat to allow sampling with both techniques simultaneously, so the resulting sample sites ranged in size from 100 -150 m^2. Habitat types were classified by water depth and the density of submerged macrophyte cover (Table 2.1). Low cover sites consisted of either bare mud or a mix of mud and the colonial algae, *Chara* spp. Medium cover sites were primarily a mix of *Chara* and *Potamogeton* spp., while high cover sites contained *Chara, Potamogeton* spp., and Eurasian watermilfoil (*Myriophyllum spicatum*). Each habitat type was represented by three sites, and each site was sampled three times over the period from 22 June to 26 August 1998.

Visual transects were performed by laying 30 m of nylon rope, weighted with bricks, in a straight line through a homogeneous habitat patch. Transects were set on the bottom at depths ranging from 0.5 - 2 m in the shallow sites, and 2 - 4 m in the deep sites. Transects in shallow sites were carried out by snorkeling; SCUBA equipment was required for deeper transects. After the laying of the transect rope, each transect was left for ten minutes to minimize the potential disturbance effect on resident fishes. A single observer swam the full length of the rope, noting all fishes located within 1 m on each side of the rope (Krebs 1989).

Gillnet sets were performed with an experimental small-mesh monofilament net, consisting of four adjacent, 1.5 m (height) x 7.6 m (width) panels of different mesh sizes (18, 36, 54, and 72 mm stretch mesh). Gillnets were set for a 1 h period, in the same homogeneous habitat patch as the visual transect, and all nets were fished on the bottom.
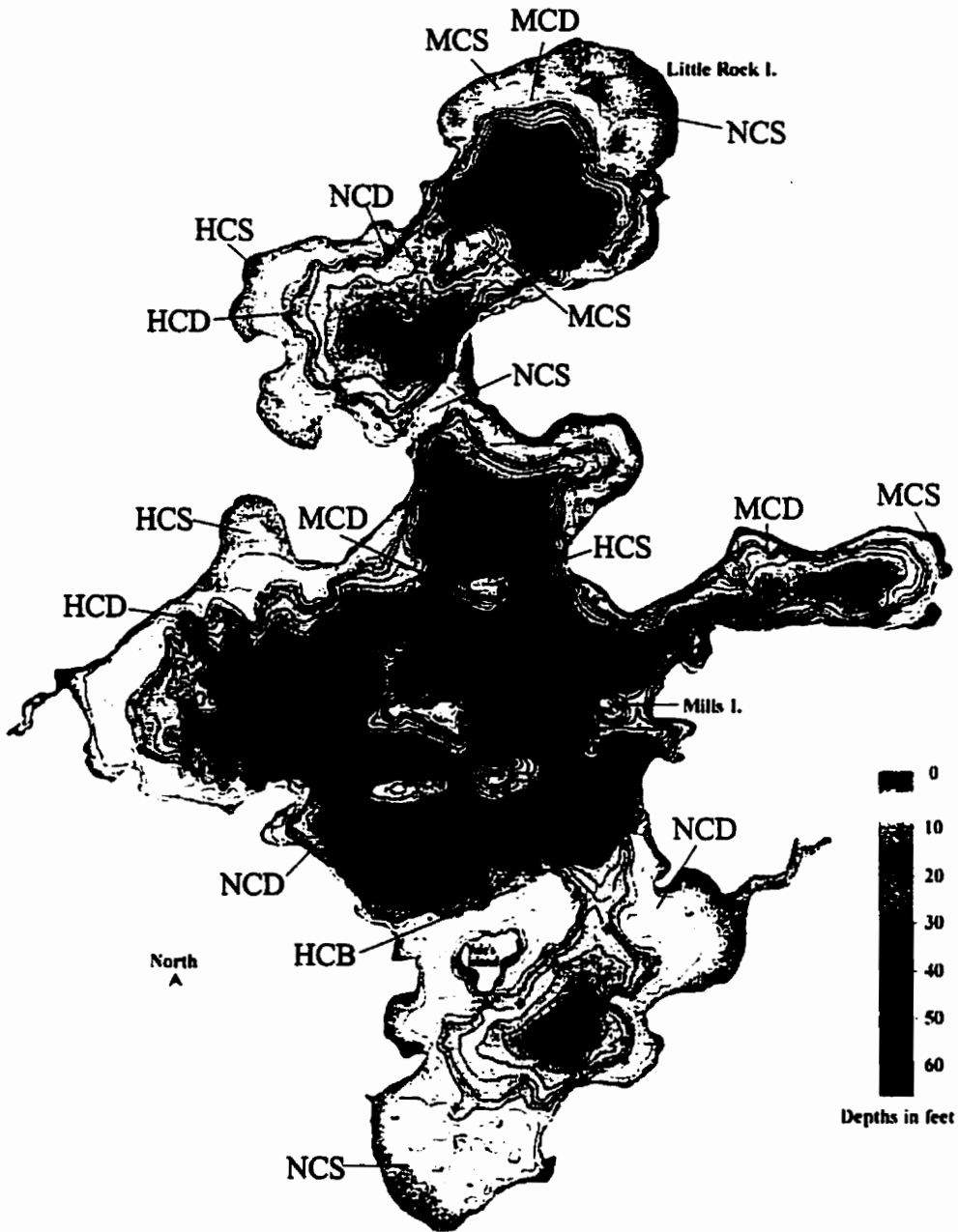
Figure 2.1. Map of Big Clear Lake, indicating the sites used for concurrent gillnet and visual transect samples. The codes represent each of the six habitat types sampled by this study; each habitat was sampled in three locations. Habitat codes are available in Table 2.1.

15

Table 2.1. Habitat classification scheme used in this study.

	Submergent cover (%)		
Depth (m)	0-5	5-15	>25
0.5-2	No cover shallow (NCS)	Medium cover shallow (MCS)	High cover shallow (HCS)
2-4	No cover deep (NCD)	Medium cover deep (MCD)	High cover deep (HCD)

Each captured individual was identified to species, measured (fork length in mm), and released. Live individuals were released at the site of capture; dead individuals (< 3% of total catch) were taken to shore and buried.

Fishes that were sampled by visual transect were also categorized by visually assessing the length of each fish observed, and assigning it to a particular life stage. For some species this simply involved classification as a juvenile or adult, but for others, young-of-year fishes could also be distinguished from juveniles. Life stages were determined by using average length at age data from Scott and Crossman (1973) for each of the species sampled during the surveys (Appendix 2.1).

Transect swims and gillnet sets were performed during daylight hours, from 10:00 AM - 6:00 PM, after the setting of an experimental gillnet in the same habitat patch. Environmental variables, such as Secchi depth, water temperature, and underwater light levels, were recorded at each site. Water temperature and light level readings were taken on the bottom at either the transect or gillnet location, while Secchi depths had to be taken in deeper locations adjacent to the actual sampling sites. Temperature readings were physically made by the observer, and recorded on the underwater slate. Light level measurements were made using Licor Radiation Sensor Li-192sa photometer.

Data analysis

The effect of light levels on the sampling ability of each technique was determined by correlating the $\log_e (x+1)$-transformed abundance with ambient light levels. Water temperature and Secchi depth readings varied little, so statistical relationships were not examined for these environmental parameters.

To assess differences in sampling ability between the visual transects and gillnet

sets and to determine whether there were any differences in gear sampling ability among

habitats, data were analyzed for species and species life stage at three numerical scales.

The importance of numerical resolution was stressed by Rahel (1990), who suggested

using three numerical scales (absolute abundance, abundance rankings, and species

presence-absence) when analyzing community data. Life stage may also be important in

fish community work, as species often undergo ontogenetic niche shifts (Werner and Hall

1988). Different sampling techniques may sample different life stages (Weaver et al.

1993); therefore, statistical analyses were not only done at the species level, but at the life

stage level as well.

The number of species and life stages sampled by gillnet sets and visual transects

were compared using a fully factorial, mixed model repeated measures analysis of

variance (ANOVA), with gear and habitat as the main factors, site as a random factor

nested within habitat, and samples from same site taken in different time periods as the

repeated measure. This allowed for the predicted differences in sampling ability of each

technique to be compared across habitats.

To compare the relative abundance of species as assessed by the two techniques,

raw data were first $\log_e (x+1)$-transformed to correct for non-normality. Relative

abundance was then calculated by converting species or species life stages counts from

each visual transect or gillnet set to a percentage. These percentages were averaged over

the three replicates at each site for each sampling method, and differences in relative

abundance across habitats were determined by averaging the calculated relative species

abundances from each habitat, and correlating the relative abundance of each species (or

18

species life stage) estimated with one sampling technique against that assessed with the other.

Ranked abundance data were also used to test for differences between sampling techniques. For these analyses, $\log_e (x + 1)$-transformed species or species life stage counts from individual assessments were first averaged by site and method, and then the species or species life stages were averaged across all sites. Spearman correlations were then used to test the relationship between ranked abundances within habitats and for all habitats combined.

Differences in sampling ability between visual transects and gillnets were examined at a third numerical scale by using species presence-absence data. Jaccard's Coefficient of Community ($CC = C / A + B - C$, where C is the number of species sampled in common, and A and B are the number of species sampled in gear types A and B, respectively; Jaccard (1901)) was utilized to test for differences between sampling techniques. Jaccard's coefficient measures the similarity of two assemblages, or in this case concurrent samples, on a scale from zero (no species in common) to one (all species in common). As similarity measures are typically noisy, replicate samples from a community often have a measured similarity of $0.6 - 0.9$ (Gauch 1982). Therefore, similarity measures were considered significant when ≥ 0.6 (Gauch 1982).

Finally, differences in sampling ability between visual transects and short-term gillnet sets were examined across habitat types using the relative abundance species life stage data in a Principal Components Analysis (PCA). The data set (27 species life stages by 108 sites) were converted to a correlation matrix (see appendix 2.2), rotated with a normalized varimax rotation, and the resulting factor loadings used to convert the

correlation matrix into factors scores for the first two principal components. The factor

scores were then plotted to determine whether the two sampling techniques could be

spatially separated.

2.3. Results

Environmental variables

Water temperature and Secchi depth varied minimally over the two month survey.

Water temperatures ranged from 22 – 25 °C, while Secchi depth readings ranged from 3.7

– 4.0 m. Ambient light levels varied greatly, ranging from 3 – 579 micromol / sec / m^2.

As one would expect, shallow habitats had higher light levels than deeper habitats (Table

2.2). However, light levels were not significantly correlated with the abundance of fishes

sampled for either the experimental gillnet (r = -0.22; n = 54; P = 0.11) or visual transects

(r = -0.18; n = 54; P = 0.19). Ambient light levels explained only 5% and 3% of the

variance in abundance for gillnet and visual transect samples, respectively.

Species and life stage comparison

A total of 2,260 individuals (1,854 by visual transects; 406 from gillnets) from 14

species were sampled by the two techniques, with 24 species life stages represented

during the survey (Table 2.3). Twelve species (21 species life stages) were observed with

visual transects, whereas only nine species (16 species life stages) were captured in

gillnets.

Table 2.2. Ambient light levels present when sampling in each of the six habitat types. Values presented are averaged from the three sites representing each habitat, and error measurements are standard error.

	Habitat type					
	NCS	MCS	HCS	NCD	MCD	HCD
Ambient light (watts / m^2)	272 (47)	214 (53)	267 (67)	83 (18)	107 (37)	60 (14)

Table 2.3. Species and their associated life stages sampled with visual transects and gillnets in Big Clear Lake; June - July, 1998

Species	Life stage[a]	Code	Sampling technique	
			Visual transect	Gillnet
Esox lucius (northern pike)	A	NPA		*
Notemigonus crysoleucas (golden shiner)	A	GSA		*
Notropis volucellus (mimic shiner)	A	MSA	*	
	YOY	MSYOY	*	
Pimephales notatus (bluntnose minnow)	A	BNMA	*	
	YOY	BNMYOY	*	
Ameirus nebulosus (brown bullhead)	A	BBHA	*	
Fundulus diaphanus (banded killifish)	A	BKA	*	
Ambloplites rupestris (rock bass)	A	RBA	*	*
Lepomis gibbosus (pumpkinseed)	A	PSA	*	*
	J	PSJ	*	*
Lepomis macrochirus (bluegill)	A	BGA	*	*
	J	BGJ	*	*
Lepomis spp.[b]	A	LEPA	*	*
	J	LEPJ	*	*
	YOY	LEPYOY	*	
Micropterus dolomieui (smallmouth bass)	A	SMBA	*	*
Micropterus salmoides (largemouth bass)	A	LMBA	*	*
	J	LMBJ	*	*
	YOY	LMBYOY	*	*
Perca flavescens (yellow perch)	A	YPA	*	*
	J	YPJ	*	*
	YOY	YPYOY	*	*
Percina caprodes (logperch)	A	LPA	*	
Stizostedion vitreum (walleye)	A	WEA		*
	J	WEJ	*	*
	YOY	WEYOY	*	

[a] Life stage classification: A = adult; J = juvenile; YOY = young-of-year

[b] Either bluegill-pumpkinseed hybrids, or individuals too small to definitively identify to species.

When catches were analyzed by species, species counts varied significantly between the two techniques as well as among habitats (Technique $F_{1,12} = 7.7$; P = 0.017; Habitat $F_{5,12} = 12.9$; P < 0.001). On average, visual transects sampled 3.0 ± 0.2 (SE) species, while gillnets sampled 2.6 ± 0.2 species. However, there was also a significant technique by habitat interaction ($F_{5,12} = 3.7$; P = 0.023), suggesting that the differences in gillnet and visual transect sampling ability were not consistent across habitats. Visual transects tended to sample more species than gillnets in all medium and high cover habitats, but the opposite trend was observed in both no cover habitats (Table 2.4a). Significantly fewer species were observed or captured in no cover, shallow habitats than in the other five habitat types (Tukey HSD, P < 0.001 in all cases); no other significant differences were observed among habitats.

The number of life stages also varied significantly between visual transects and experimental gillnets, as well as among habitat types (Technique $F_{1,12} = 15.7$; P = 0.007; Habitat $F_{5,12} = 19.0$; P = 0.003). The mean number of life stages observed by visual transects was 4.0 (± 0.3), while the mean number of life stages sampled by gillnet was 3.3 (± 0.3). As was the case with species, the relative ability of the two techniques to sample life stages varied among habitats (Technique * Habitat interaction: $F_{5,12} = 11.3$; P = 0.009). Once again, visual transects tended to sample more species than gillnets in all medium and high cover habitats, but the opposite trend was observed in both no cover habitats (Table 2.4b).

Table 2.4. Comparison of the mean number (± SE) of (a) species, and (b) species life stages sampled by visual transects and gillnets in each habitat type. Three sites were sampled in each habitat, and each site was sampled three times over the period of study.

(a) Mean number of species

Habitat	Visual transects	Gillnet sets
No cover shallow	0.6 (0.1)	0.9 (0.2)
No cover deep	2.8 (0.3)	3.3 (0.2)
Medium cover shallow	3.7 (0.1)	2.3 (0.4)
Medium cover deep	3.4 (0.2)	2.9 (0.3)
High cover shallow	3.9 (0.4)	3.0 (0.2)
High cover deep	3.7 (0.1)	3.0 (0.3)

(b) Mean number of species life stages

Habitat	Visual transects	Gillnet sets
No cover shallow	0.6 (0.1)	1.2 (0.4)
No cover deep	3.7 (0.5)	4.3 (1.6)
Medium cover shallow	4.9 (0.6)	3.0 (0.5)
Medium cover deep	4.6 (0.2)	3.9 (1.1)
High cover shallow	5.4 (0.6)	3.8 (0.5)
High cover deep	5.0 (0.1)	3.6 (0.2)

Five species (mimic shiner *Notropis volucellus*, bluntnose minnow *Pimephales notatus*, banded killifish *Fundulus diaphanus*, brown bullhead *Ameirus nebulosus*, and logperch *Percina caprodes*) were detected only by visual transects, while two species (northern pike *Esox lucius* and golden shiner *Notemigonus crysoleucas*) were captured in gillnets and were not observed by visual transects. The most abundant species observed with visual transects were pumpkinseed *Lepomis gibbosus* (24% of all species observed), bluegill *Lepomis macrochirus* (20%), yellow perch *Perca flavescens* (17%), and bluntnose minnow (13%) (Figure 2.2). Yellow perch (37%), bluegill (12%), and pumpkinseed (10%) were also among the most abundant species sampled by gillnet, but largemouth bass *Micropterus dolomieui* were much higher in relative abundance in gillnet samples (18% vs 3% in visual transects).

Relative abundance

A significant positive correlation was found between the mean percent abundance of a species observed in visual transects and its mean percent abundance in gillnet sets across habitat types (r = 0.53, P = 0.044). This relationship weakened at the species life stage level (r = 0.38, P = 0.055). Within habitats, analysis of relative abundance indicated a significant positive correlation between visual transects and gillnet sets for only one habitat (2 - 4 m depth, no cover) at both the species and species life stage level (Table 2.5). Analysis for the other five habitats indicated only weak, non-significant correlations at both the species and the species life stage level (Table 2.5).
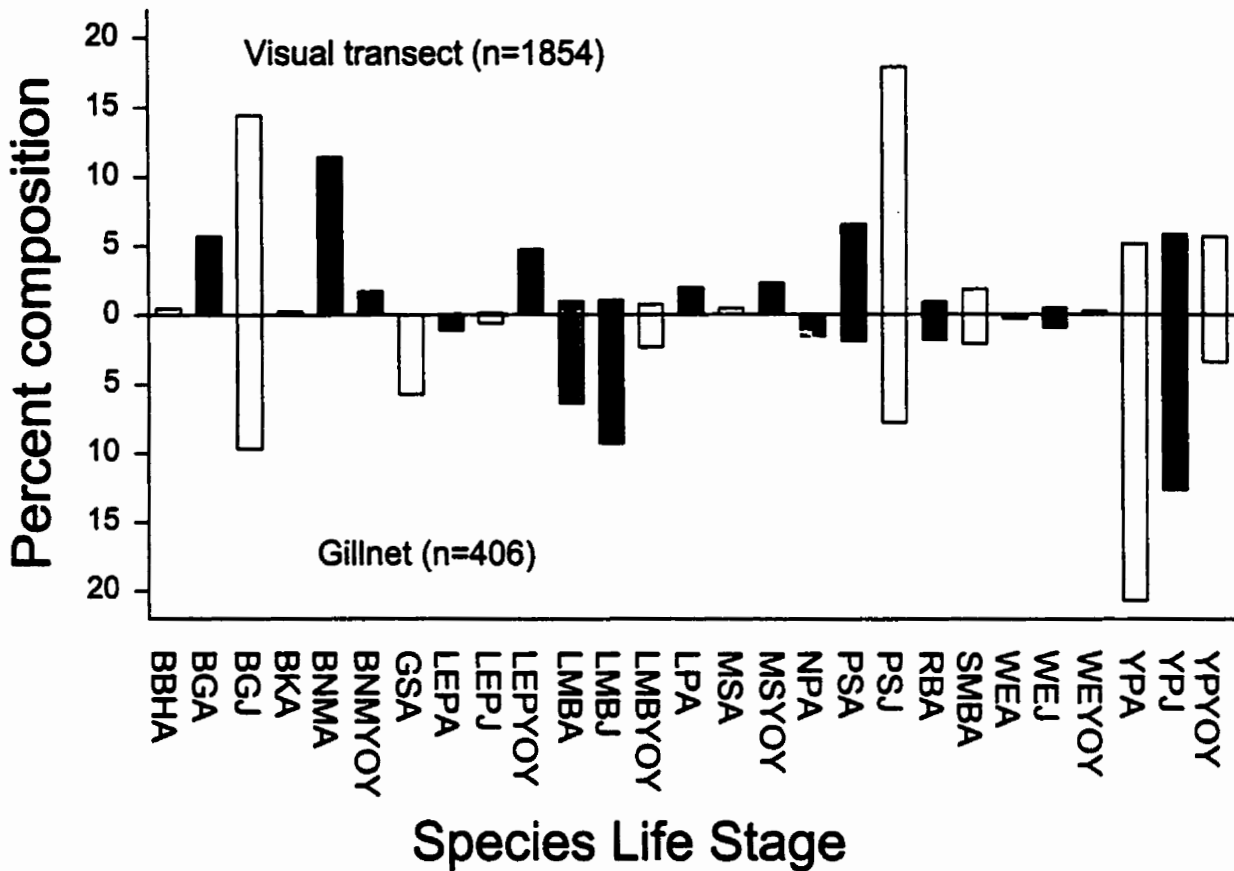
Figure 2.2. Comparison of the fish community composition in the littoral zone of Big Clear Lake, as assessed with visual transects and by gillnetting. Percent composition was calculated for each sample (18 per method), and these were averaged over all samples taken in each gear in the lake. Numbers shown are the total number of fish observed or caught with each method. Key for species life stages is provided in Table 2.3.

Table 2.5. Within-habitat correlations of the relative abundance of species and species

life stages as determined by visual transect and gillnet sampling.

Habitat	Species	Species life stage
No cover shallow	r = 0.008; n = 8; P=0.99	r = -0.41; n =11; P = 0.22
No cover deep	r = 0.69; n = 11; P = 0.02*	r = 0.52 n = 20; P = 0.02*
Medium cover shallow	r = 0.23; n = 11; P = 0.50	r = -0.02; n = 17; P = 0.95
Medium cover deep	r = 0.38; n = 9; P = 0.31	r = 0.28; n = 18; P = 0.27
High cover shallow	r = 0.03; n = 10; P = 0.93	r = -0.10; n = 16; P = 0.71
High cover deep	r = 0.47; n = 10; P = 0.17	r = 0.41; n = 19; P = 0.08

Ranked abundance

There were weak, non-significant relationships observed in species ranking between the two sampling techniques across habitat types at both the species or species life stage level of analysis (species: $r_s = 0.42$, $P = 0.12$; species life stage $r_s = 0.34$, $P = 0.08$). Within habitats, analysis of the ranked data indicated that community composition, as assessed by the two sampling techniques, was different at both the species and the species life stage level. All of the within-habitat correlations between rank abundance of species determined by the two methods were weak and non-significant. There were no significant correlations at the species life stage level either, and in shallow habitat with no cover, rank abundance with the two methods gave a nearly significant negative correlation (Table 2.6).

Presence-absence

Jaccard's Similarity Coefficient for the presence-absence matrix of species recorded with visual assessment and gillnetting was 0.50; the corresponding value at the species life stage level was 0.54. These results indicate that the community composition determined by the two sampling techniques across habitats are dissimilar. Within habitat analysis of presence-absence data also indicates that the visual assessment and gillnetting provide different assessments of the fish community. No habitat at either the species or species life stage level had a Jaccard's Similarity Coefficient ≥ 0.6 for the presence-absence matrix of species recorded with two techniques (Table 2.6).

Table 2.6. Within-habitat correlations of the rank abundance of species and species life stages as determined by visual transect and gillnet sampling. Also, an assessment of similarity between the two sampling methods, based on the presence-absence of species and species life stages.

	Species only data		Species life stage data	
Habitat	Spearman rank correlation	Jaccard's coefficient (CC)	Spearman rank correlation	Jaccard's coefficient (CC)
NCS	r_s = -0.29, n = 8, P = 0.46	0.25	r_s = -0.56, n = 11, P = 0.07	0.09
MCS	r_s = -0.05, n = 11, P = 0.88	0.46	r_s = 0.10, n = 17, P = 0.69	0.47
HCS	r_s = 0.15, n = 10, P = 0.66	0.50	r_s = -0.12, n = 16, P = 0.66	0.50
NCD	r_s = 0.35, n = 11, P = 0.28	0.45	r_s = 0.21, n = 20, P = 0.38	0.40
MCD	r_s = 0.39, n = 9, P = 0.29	0.56	r_s = 0.10, n = 18, P = 0.69	0.44
HCD	r_s = 0.57, n = 10, P = 0.08	0.50	r_s = 0.07, n = 19, P = 0.76	0.42

PCA analysis

Visual interpretation of the PCA data suggested a potential separation of the two sampling techniques (Figure 2.3). However, the two most significant axes explained only 15% of the total variance, and the species that loaded heavily on Factor 2, the axis that most separated the sampling techniques, were rarely sampled by either method (Table 2.7). These suggest that the separation apparent in Figure 2.3 is not meaningful.

2.4. Discussion

The results of this study show that visual transects and short-term small-mesh experimental gillnet sets produce different assessments of a littoral zone fish community. Despite testing for community similarities between sampling techniques with species and species life stage data across habitat types at three numerical levels, a significant degree of similarity was rarely achieved (only 3 of the 42 analyses undertaken indicated significant sampling similarities between techniques). The prediction that visual transects would sample more species and species life stages, and thus provide a more complete picture of the fish community than gillnets, was generally supported. Visual transects sampled significantly more species and life stages across habitat types. However, the sampling patterns of the two species were not consistent among habitats. Visual transects sampled more species and life stages in habitats with macrophyte cover, but the experimental gillnet sampled more species and life stages in no cover habitats.

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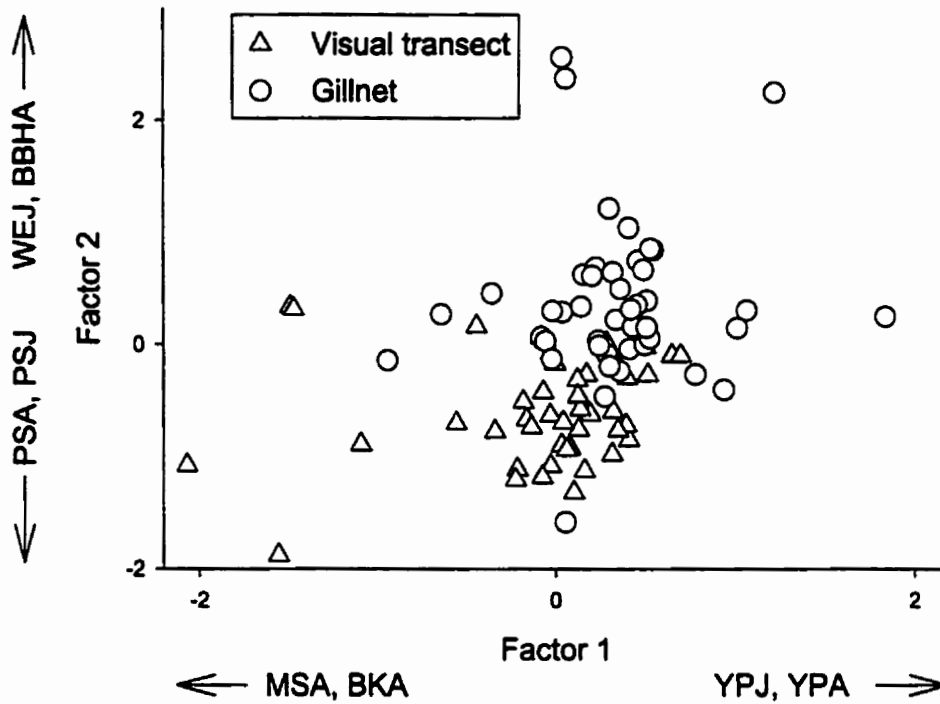
Figure 2.3. The spatial separation of experimental gillnet and visual transect samples. The relative abundance values of each concurrent gillnet and visual transect sample were transferred to a correlation matrix by principal components analysis (PCA), and the resulting matrix compared against factor scores created by the PCA to produce the above Figure. Species life stages contributing most to each Factor are presented above; species life stage codes can be found in Table 2.3.

Table 2.7. The factors scores obtained from the life stage correlation matrix. Scores indicate the relative importance of each life stage in separating the data matrix. Species life stage codes are in Table 2.3.

Species life stage	Factor 1	Factor 2
BBHA	-0.096	-0.552
BGA	0.168	0.169
BGJ	0.131	0.008
BKA	-0.722	-0.096
BNMA	-0.344	0.300
BNMYOY	0.008	0.128
GSA	0.054	-0.209
LEPHYBA	-0.024	-0.458
LEPHYBJ	0.175	-0.028
LEPYOY	0.037	0.113
LMBA	0.120	-0.422
LMBJ	0.017	-0.076
LMBYOY	0.005	0.032
LPA	-0.075	-0.020
MSA	-0.825	0.047
MSYOY	0.004	0.021
NPA	0.237	-0.118
PSA	-0.099	0.431
PSJ	0.049	0.415
RBA	0.175	0.018
SMBA	-0.006	-0.009
WEA	0.118	-0.218
WEJ	-0.081	-0.712
WEYOY	-0.362	0.208
YPA	0.236	-0.299
YPJ	0.258	0.071
YPYOY	-0.492	-0.066

The higher number of species sampled by visual transects is consistent with results obtained in other freshwater gear comparison studies that have examined visual methods as one sampling alternative (Goldstein 1978, Rossier 1997). In fact, even higher numbers of species and species life stage counts would be expected if a non-linear visual method is employed (Kimmel 1985, Sanderson and Solonsky 1986). Some underwater visual techniques do not rely on the laying of a visual transect, and instead obtain species / time relationships, as opposed to the species / area relationships found by linear techniques. Such techniques typically provide broader community coverage, at the expense of abundance estimates.

The ability of gillnets to capture more species and life stages than visual transects in no cover habitats may be explained by the behaviour of species that inhabit low cover or open water areas. Species that are typically found in open water are more likely to flee an approaching observer than species associated with structure (Sale and Douglas 1981, Brock 1982). Thus, the significant shift in sampling ability across habitat types demonstrated by this study suggest that gillnets may be more useful for sampling fishes that prefer habitats that are sparse in macrophyte cover.

Some of the observed differences between sampling techniques can undoubtedly be explained by the inability of gillnets to sample small fishes, despite the small mesh sizes employed by this study. Banded killifish, mimic shiners, and the young-of-year of many species were likely too small to be captured even by the smallest mesh size (Hansson and Rudstam 1995). Much of the research conducted to determine community patterns in freshwater lakes have relied on sampling gear that select primarily for larger, managed species (e.g. Tomas and Haas 1995, Lester et al. 1996, Peltonen et al. 1999).

33

The results of this study suggest that some species would be missed with these methods, resulting in an incomplete community profile.

Fish ecologists interested in addressing questions requiring a broad community survey, over a wide size range of body sizes, would be better served by an underwater visual technique. Marine researchers long ago realized the necessity of conducting studies at a finer spatial scale when investigating coral reef fish assemblages (Brock 1954, Odum and Odum 1955), and since that time, alternate visual techniques have been developed, debated, and improved upon (Jones and Thompson 1978, Sale and Douglas 1981, DeMartini and Roberts 1982, Kimmel 1985, Bohnsack and Bannerot 1986, Sanderson and Solonsky 1986). Despite being a relatively under-employed technique, some freshwater researchers have utilized underwater visual methods, especially for determining species microhabitat use, behaviour, and spatial segregation (e.g. Hall and Werner 1977, Keast and Harker 1977, Chipps et al. 1994, Walters and Wilson 1996). In my study, visual transects were able to sample both predator and prey species effectively, while the experimental gillnet failed to sample a number of prey fishes. Thus, underwater visual methods appear a more effective tool for community-level surveys in waterbodies where the use of such techniques is possible.

Both visual observations and gillnet sets introduce sampling biases unique to each method. It has been established that gillnets fish selectively, with larger mesh sizes able to capture a wider size range of fish than smaller mesh sizes. Smaller mesh sizes are also less efficient than larger mesh sizes at catching fish, as small fish are less likely to be retained after contact with the net (Hamley 1975). As already noted, many of the species and life stages missed by gillnet sampling in this study were small (mostly cyprinids or

34

young-of-year of other species), suggesting that mesh selectivity may have played a role in reduced number of species caught in gillnets. Analysis of smallmesh gillnet size-selectivity on herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) indicated that our smallest mesh size would likely not have been capable of capturing non-gibbose fish < 80 mm (Hansson and Rudstam 1995). However, only two of the five species not sampled in our gillnet sets (mimic shiner and banded killifish) were too small to be sampled in the smallest mesh of the net, which suggests that the reduced number of species captured in gillnets cannot be attributed to mesh size alone.

Visual methods are also subject to potential observer bias, as large individuals and rare species have been shown to direct observer attention (Rossier 1997). In addition, cryptic and transient-pelagic species are expected to escape detection by underwater observers (Sale and Douglas 1981, Brock 1982). The two species sampled by gillnets but not observed by visual transects fit into these categories. The golden shiner is an open water planktivore, and is likely predisposed to avoiding large moving objects in open water, while northern pike are well camouflaged, and only likely to be spotted if physically disturbed by the observer.

The effectiveness of both sampling techniques can be influenced by a variety of physical and chemical factors. Underwater visual techniques are entirely reliant on good visibility, as the ability to see fishes reduces significantly as visibility decreases (Palmer and Greybill 1986, Dolloff et al. 1996). Visibility is also an important factor in gillnet catches, as some species alter their movement patterns with changes in turbidity. Activity level is an important component of the ability of gillnets to capture fish, so increasing (Wright and O'Brien 1984) or decreasing (Hansson and Rudstam 1995)

activity in response to increasing turbidity can influence gillnet success. The visibility in this study remained consistently high over the two month sampling period, however, making it unlikely that changes in visibility affected the outcome of this study. Water temperature plays a similar role in both techniques by reducing fish activity. Colder water temperatures make it more difficult to observe and capture fishes (Hillman et al. 1992, Hubert 1983), but the warm temperatures maintained over the duration of this study mean it is not likely that either the experimental gillnets or visual transects were affected by this parameter. One parameter that is capable of influencing both visual transects and gillnets that varied greatly among sites is ambient light level. Light level can affect the ability of fishes to see, and therefore avoid, gillnets (Cui et al. 1991), and are an important component of underwater visibility. However, light levels were not important in explaining the variation in abundance for either technique in this study. Thus, physical factors did not seem to affect the sampling ability of either technique in this study.

While there were not many inconsistencies among analyses for sampling technique differences at the three numerical levels addressed by this study, the results do indicate that addressing sampling scale is an important part of determining proper sampling procedures. In general, analyses at the species level indicated more similar communities than those at the species life stage level. Few researchers have investigated fish communities by categorizing species into life stages (Weaver et al. 1993). Not doing this could lead to misinterpretations about habitat use, as many fish species undergo ontogenetic habitat shifts (Werner and Hall 1988).

While most studies find relative abundance levels to be the least likely to show differences in species richness (Rahel 1990), this study showed that total abundance was at least as likely, if not more so, to indicate significant similarity between sampling techniques as abundance rankings and species presence/absence. This result was unexpected, as decreasing numerical resolution (e.g. using similarity measures) typically increases the probability of finding significant overlap (Williamson 1981, Ogden and Ebersole 1981, Moyle and Vondracek 1985). However, similar patterns across numerical scales were noted in a watershed where the fauna was relatively depauperate and dominated by a few common species, and where rare species were variable in their occurrence (Lohr and Fausch 1997). These characteristics are shared by the fish community of Big Clear Lake.

In conclusion, this study demonstrated that comparisons of fishes obtained by underwater visual transects and short-term experimental gillnet sets, when sampled concurrently in a homogeneous habitat patch, rarely resulted in a significant species overlap between the techniques. Visual transects sampled more species and life stages, though the relative sampling ability of the two techniques changed depending on the presence or absence of macrophyte cover. If the question of interest involves sampling a broad size range of fishes in primarily vegetated littoral zone habitats, the results of this study indicate that underwater visual observations provide greater species and life stage coverage than experimental gillnets.

Appendix 2.1. Classification of life stages sampled based on length (data from Scott and Crossman 1973). Species with short life spans were considered as only YOY or adult.

Species	Approximate length (mm)		
	YOY	juvenile	adult
northern pike	<150	150 - 300	>300
mimic shiner	<30	-	>30
bluntnose minnow	<35	-	>35
golden shiner	<50	-	>50
brown bullhead	<200	-	>200
banded killifish	<40	-	>40
pumpkinseed	<30	30 - 110	>110
bluegill	<30	30 - 120	>120
smallmouth bass	<45	45 - 250	>250
largemouth bass	<50	50 - 250	>250
rock bass	<40	40 - 200	>200
yellow perch	<40	40 - 140	>140
walleye	<180	180 - 300	>300
logperch	<35	-	>35

Appendix 2.2. Correlation matrix used to generate factors scores, which were used to determine whether the relative abundance of experimental gillnet sets and underwater visual transects could be spatially separated.

	BBHA	BGA	BGJ	BKA	BNMA	BNMYOY	GSA	LEPHYBA	LEPHYBJ	LEPYOY	LMBA	LMBJ	LMBYOY	LPA	MSA	MSYOY	NPA	PSA	PSJ	RBA	SMBA	WEA	WEJ	WEYOY	YPA	YPJ	YPYOY
BBHA	1	-0.05	0.06	-0.01	-0.04	-0.02	-0.02	-0.02	-0.01	-0.02	0.19	-0.04	-0.01	-0.01	-0.02	-0.01	-0.02	-0.04	-0.07	-0.02	-0.01	-0.01	0.57	-0.01	-0.07	-0.06	-0.03
BGA	-0.05	1	0.22	-0.05	-0.08	-0.01	-0.12	0.02	-0.07	0.03	-0.07	-0.06	-0.05	-0.05	-0.04	-0.06	-0.07	0.07	-0.03	0.03	-0.04	-0.05	-0.08	-0.03	-0.08	-0.09	-0.11
BGJ	0.06	0.22	1	-0.05	-0.06	-0.01	-0.13	0.01	-0.08	-0.05	-0.03	-0.03	-0.07	-0.06	-0.09	-0.06	-0.08	-0.1	-0.17	0.05	-0.08	-0.05	-0.03	-0.08	-0.14	-0.14	-0.1
BKA	-0.01	-0.05	-0.05	1	0.02	-0.02	-0.02	-0.02	-0.01	-0.03	-0.04	-0.04	-0.01	0.03	0.61	-0.01	-0.02	-0.04	-0.07	-0.02	-0.01	-0.04	-0.06	-0.01	-0.07	-0.06	0.35
BNMA	-0.04	-0.08	-0.06	0.02	1	0	-0.09	0.01	-0.05	-0.09	-0.04	-0.03	-0.03	-0.04	0.3	-0.04	-0.07	-0.03	0.06	-0.06	-0.06	-0.03	-0.04	-0.02	-0.16	-0.09	-0.07
BNMYOY	-0.02	-0.01	-0.01	-0.06	0	1	-0.04	0.1	0.01	-0.03	-0.06	0.02	0.29	-0.02	0.3	-0.05	-0.01	-0.04	-0.02	-0.1	-0.04	-0.02	0.08	0.11	-0.12	-0.01	-0.02
GSA	-0.02	-0.12	-0.13	-0.02	-0.09	-0.04	1	-0.03	0.13	0.13	-0.08	-0.01	-0.05	-0.03	-0.03	-0.03	-0.02	-0.02	-0.14	-0.04	-0.03	-0.02	0.38	-0.03	0.02	0.1	-0.04
LEPHYBA	-0.02	0.01	0.01	-0.02	0.01	-0.04	0.1	1	-0.01	0.1	0	0	-0.02	-0.02	-0.02	-0.02	-0.03	-0.03	-0.1	-0.05	-0.04	-0.01	-0.02	-0.02	-0.07	0.08	-0.04
LEPHYBJ	-0.01	-0.07	-0.08	-0.01	-0.05	-0.03	0.13	-0.01	1	-0.03	-0.05	-0.05	-0.02	-0.01	-0.02	-0.02	-0.02	-0.03	-0.02	-0.02	-0.03	-0.02	-0.02	-0.02	-0.12	-0.07	-0.04
LEPYOY	-0.02	0.03	-0.05	-0.03	-0.09	-0.03	0.13	0.29	-0.03	1	-0.07	-0.07	-0.03	-0.02	-0.03	-0.03	-0.04	0.07	-0.18	-0.05	-0.05	-0.03	-0.03	-0.05	-0.05	-0.05	-0.07
LMBA	0.19	-0.07	-0.05	-0.03	-0.11	-0.06	-0.08	-0.05	-0.07	-0.06	1	-0.06	-0.04	-0.03	-0.06	0.01	0.07	-0.12	0.02	0.02	-0.05	0.27	0.07	-0.05	0.16	-0.05	-0.03
LMBJ	-0.04	-0.06	-0.03	-0.04	-0.09	-0.03	-0.03	-0.03	-0.04	-0.06	1	1	-0.03	-0.04	0.01	-0.04	-0.07	-0.12	-0.18	0.02	0.02	-0.04	-0.04	-0.01	-0.01	-0.08	-0.03
LMBYOY	-0.01	-0.05	-0.07	-0.01	-0.06	0.29	-0.01	0	-0.01	-0.03	-0.03	-0.03	1	-0.02	-0.02	-0.02	-0.05	-0.03	0.02	0.02	-0.03	-0.01	-0.01	-0.02	-0.06	-0.08	-0.01
LPA	-0.01	-0.05	-0.06	0.03	-0.03	-0.04	-0.02	-0.02	-0.03	-0.05	-0.06	-0.02	-0.02	1	0.01	-0.02	-0.01	-0.02	-0.07	-0.04	-0.01	-0.01	-0.01	-0.01	-0.07	0.05	-0.01
MSA	-0.02	-0.04	-0.09	0.61	0.3	0.01	-0.03	0.02	-0.02	-0.03	-0.04	0.01	-0.02	0.01	1	1	-0.02	-0.03	-0.1	-0.04	-0.02	-0.02	0.27	0.37	-0.08	-0.08	0.19
MSYOY	-0.01	-0.06	-0.06	-0.01	-0.04	-0.05	-0.03	-0.01	-0.02	-0.03	-0.04	-0.04	-0.01	-0.02	-0.02	1	-0.02	-0.03	-0.03	-0.03	-0.01	0.35	0.35	-0.03	0.08	0.09	-0.05
NPA	-0.02	-0.07	-0.08	-0.02	-0.07	-0.08	-0.04	-0.03	0.5	-0.05	-0.07	-0.07	-0.05	-0.03	-0.02	-0.02	1	-0.08	0	0	-0.04	-0.06	-0.04	0.12	0.01	0.01	-0.1
PSA	-0.04	0.07	-0.1	-0.04	0.2	0.02	-0.02	-0.03	-0.05	-0.07	-0.12	-0.12	-0.05	-0.04	0.08	-0.03	-0.08	1	0.2	-0.09	-0.06	-0.04	-0.07	-0.12	0.12	0.12	-0.1
PSJ	-0.07	-0.03	-0.17	-0.07	0.06	-0.02	-0.14	-0.1	-0.02	-0.07	-0.18	-0.18	-0.07	-0.07	-0.1	-0.03	0	0.2	1	-0.02	-0.1	-0.07	-0.12	0.21	0.21	-0.07	-0.06
RBA	-0.02	0.03	0.05	-0.02	-0.06	-0.04	-0.04	-0.04	-0.04	-0.04	0.02	0.02	0.02	-0.02	-0.04	-0.04	0	-0.09	-0.02	1	-0.04	-0.1	-0.04	-0.04	-0.1	0.09	-0.07
SMBA	-0.01	-0.04	-0.08	-0.01	-0.06	-0.03	-0.03	-0.02	-0.01	-0.02	-0.05	-0.05	-0.02	-0.01	-0.02	-0.02	-0.01	-0.06	-0.1	-0.04	1	-0.01	-0.01	-0.02	-0.09	-0.09	-0.04
WEA	-0.01	-0.05	-0.05	-0.01	-0.01	-0.02	-0.03	-0.03	-0.02	-0.01	-0.04	-0.04	-0.03	-0.01	-0.03	-0.03	-0.01	-0.02	-0.04	-0.02	-0.01	1	-0.02	-0.01	-0.08	-0.06	-0.04
WEJ	0.57	-0.08	-0.03	-0.06	-0.03	0.08	0.38	0.38	-0.01	-0.02	-0.06	-0.04	-0.03	-0.02	-0.04	-0.04	-0.07	-0.12	-0.04	-0.02	-0.01	-0.02	1	-0.02	-0.01	-0.01	-0.05
WEYOY	-0.01	-0.03	-0.08	-0.01	-0.02	0.11	-0.02	0.21	-0.02	-0.03	0.01	-0.01	-0.02	-0.01	-0.01	-0.02	0.12	0.21	-0.12	-0.03	-0.02	-0.01	-0.02	1	-0.02	0.11	-0.01
YPA	-0.07	-0.03	-0.08	-0.07	-0.01	0.11	0.08	-0.01	0.23	-0.05	0.16	0.05	-0.05	-0.07	-0.08	-0.08	-0.02	0.08	-0.07	0.03	-0.08	-0.09	-0.01	0.11	1	-0.07	-0.08
YPJ	-0.06	-0.09	-0.14	-0.06	-0.09	-0.01	0.1	0.1	-0.1	-0.05	-0.01	-0.01	-0.08	-0.07	-0.08	-0.09	-0.01	0.09	-0.02	0.09	-0.09	0.11	0.11	-0.07	1	1	-0.11
YPYOY	-0.03	-0.11	-0.1	0.35	-0.07	-0.02	-0.04	-0.04	-0.04	-0.05	-0.07	-0.03	-0.01	-0.06	0.19	-0.05	-0.1	-0.1	-0.06	-0.07	-0.04	-0.04	-0.03	-0.05	0	-0.13	1

39

Chapter 3.

Biotic Influences on Habitat Selection by Young-of-Year Walleye (*Stizostedion vitreum*) in the Demersal Stage

3.1. Introduction

The importance of habitat selection on the variable recruitment patterns observed in most fishes may not be readily apparent. A mounting body of evidence suggests that juvenile fishes should attempt to maximize growth rates, as mortality decreases with increasing body size (Peterson and Wroblewski 1984, Houde 1987, Houde 1989, review by Sogard 1997). Thus, one might expect juvenile fishes to reside in habitats that provide the greatest potential for growth. However, size-selective predation has been identified as one of the primary mechanisms behind size-selective mortality in juvenile fishes (Chevalier 1973, Post and Evans 1989a), and habitats with the highest potential for growth often have the highest predation risk (Werner et al. 1983a, 1983b). Typically, habitats with high structural complexity tend to have lower predation rates as they provide more refuge opportunity for prey fishes (Savino and Stein 1982, Werner et al. 1983b, Gotceitas and Colgan 1990). Therefore, juvenile fishes have been predicted to select habitats that minimize mortality in relation to foraging return (Gilliam and Fraser 1987). For many juvenile freshwater fishes, this means utilizing sub-optimal foraging habitats or altering foraging behaviour in order to reduce predation risk to an acceptable level (Werner et al. 1983b, Abrahams and Dill 1989, Gotceitas and Colgan 1990). Therefore, faster growing fish may survive better within a habitat type, but not across populations if the fastest growing individuals reside in the riskiest habitats (Sogard 1997).

A general pattern of risky life stages residing in structurally complex habitats is apparent in a number of fish species (Werner et al. 1983b, Anderson 1984, McIvor and Odum 1988, Rozas and Odum 1988, Nelson and Bonsdorff 1990, Eklöv 1997). However, there are some species that appear to favour areas of high prey availability over refuge (Miltner et al. 1995, Leis and Fox 1996), and others that are fortunate enough to have both high prey availability and low predation risk in the same habitat (Rozas and Odum 1988).

Species that grow quickly face a series of transitional ecological requirements early in their development. This is undoubtedly true for young-of-year (YOY) walleye (*Stizostedion vitreum*), which undergo a series of ontogenetic shifts during their first year of life. Walleye eggs hatch in early spring, and the YOY are initially pelagic planktivores, consuming increasingly larger zooplankton as they grow (Graham and Sprules 1992). Though the exact timing of the ontogenetic shift varies in the waterbody, YOY walleye ultimately become demersal and piscivorous. In one particularly well-studied population, this transformation usually occurs in late June (Houde and Forney 1970). YOY walleye then grow rapidly, often achieving lengths in excess of 200 mm in their first year of life (Scott and Crossman 1973). Piscivores, such as walleye, that face a number of shifts in ontogeny compete with species early in their life history that they will eventually prey upon (Werner and Gilliam 1984). The requirements of such a relatively complex life history are assumed to constrain piscivores into being poor competitors during their early life stages (Werner and Gilliam 1984, Persson 1988); therefore, piscivores may be more likely to favour risky habitats because they are particularly sensitive to the benefits of rapid growth.

41

To date, the lack of habitat preferences identified for YOY walleye (reviewed by Kerr et al. 1997) has led researchers to conclude that young walleye are habitat generalists, with no specific preferences after the commencement of the demersal stage. For example, studies on riverine populations have shown YOY walleye are very flexible in their early habitat choice (Stevens 1990, Leis and Fox 1996), and that these generalist tendencies continue until late summer. YOY walleye were almost ubiquitous in a Bay of Quinte survey by Savoie (1983), though sandy sites produced the greatest numbers in other Ontario lakes (Ritchie and Colby 1988). The one trend that is apparent in these studies is that YOY walleye are not typically found in heavily vegetated sites, probably because such sites are used by ambush predators such as largemouth bass (*Micropterus salmoides*) (Santucci and Wahl 1993). This notion is supported by a negative relationship between hatchery walleye fingerling success and lakes with high macrophyte cover (Seip 1995).

There are several possible explanations for the apparent generalist tendencies of young walleye. One possibility may involve the sampling techniques traditionally used for YOY walleye collection. These include seines, trawls, and electrofishers (e.g. Savoie 1983, Stevens 1990, Leis and Fox 1996), which generally sample at too broad a spatial scale to determine microhabitat preference. Species microhabitat preferences are most effectively sampled with visual techniques (Sale 1980), although relatively few researchers have used underwater methods to determine habitat preferences in freshwater (but see Chipps et al. 1994, Walters and Wilson 1996, Eklöv 1997). In addition, the distribution of YOY walleye may also be more strongly influenced by biotic factors than previously believed. Leis and Fox (1996) found that YOY walleye in a northern Ontario

42

river were more closely associated with their prey than with any particular habitat type. This observation would support the suggestion that walleye may favour areas of high prey density over refuge habitats in order to facilitate rapid early growth, and would also explain the habitat generalist tendencies of young walleye. As walleye recruitment and growth were found to be regulated by the availability of suitable prey items (Forney 1977), and the switch to piscivory is critical for YOY walleye survival (Forney 1976), it seems possible that food requirements could force young walleye to act as habitat generalists, especially if the preferred prey species are located in many different habitats. A variety of underwater visual techniques have been developed which allow researchers to determine relative species abundance (e.g. Brock 1955, Jones and Thompson 1978, Bohnsack and Bannerot 1986) making an assessment of the biotic influence on microhabitat selection possible.

The goals of this study were to assess habitat selection of YOY walleye in a lacustrine environment, and to determine whether habitats used by young walleye are related to the distribution of their predators or prey. The primary objective of this study was to test hypotheses about walleye distribution during the demersal phase of their early life history, a critical period that can strongly influence recruitment variability in this species (Forney 1976). I hypothesized that YOY walleye would be habitat generalists; that their distribution is positively related to that of their prey; and that their distribution would be negatively related to that of their predators. My secondary objective was to examine the shoaling patterns of young walleye in these habitats; in particular, to determine the species composition of shoals that included young walleye, and whether there were changes in shoaling patterns that accompanied habitat shifts.

43

3.2. Methods

Study Site

This study was performed on Big Clear Lake (44° 43' W, 76° 55' N), a 337 ha waterbody located near the town of Arden, Ontario, Canada (Figure 3.1). The surrounding basin is typical of the Precambrian Shield formation, with rock outcroppings and thin pockets of sandy soil. Big Clear Lake is a headwater lake fed by two major inflow streams, with one drainage outlet. The lake itself consists of a number of large bays, roughly divided into four interconnected basins. Irregular glacial scouring has led to the formation of numerous small islands and shoals located throughout the lake, resulting in a large and diverse littoral zone. The combination of high habitat diversity and a strong, naturally reproducing walleye population make Big Clear Lake an excellent lake for this study.

Big Clear Lake is relatively shallow (mean depth = 6.6 m), and thermally stratified from May to November. Water quality parameters for Big Clear Lake are typical of a mesotrophic waterbody in Canada (pH = 8.3, total dissolved solids = 145 mg/L, total phosphorus = 15 ug/L (unpublished data, Ontario Ministry of the Environment 1984). Surface water temperature ranged from 18 - 26°C during the study, while Secchi depths ranged from 3.5 - 4.1 m.

Habitat Assessment and Classification Procedure

YOY walleye habitat preference and predator and prey associations were assessed using a modification of the rapid visual technique (RVT) introduced by Jones and

To Ottawa

To Peterborough   Big Clear Lake
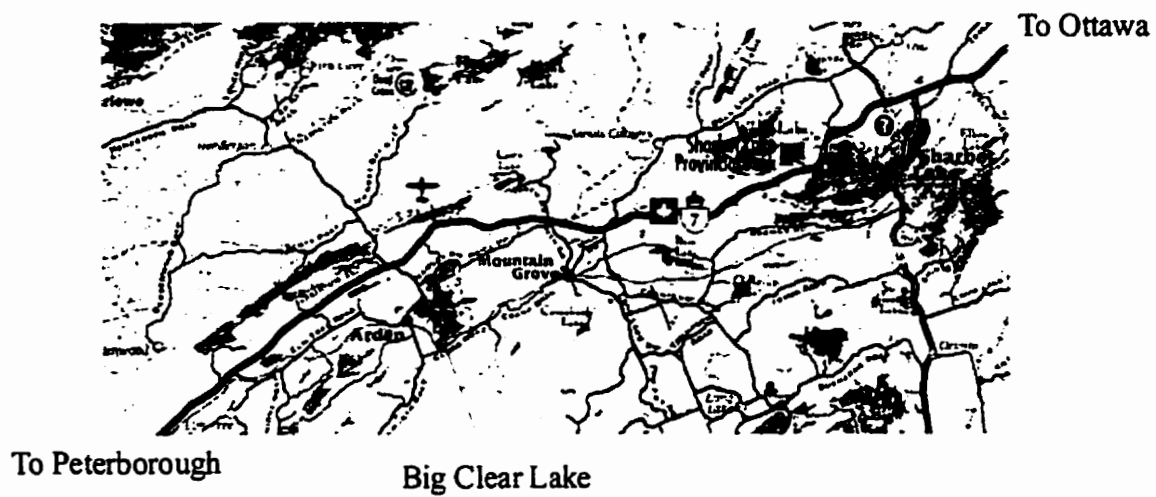
Figure 3.1. Geographic location of study lake.

Thompson (1978). The RVT was developed as an alternative to the straight-line underwater transect, with divers searching a pre-determined area for a specific length of time (Jones and Thompson 1978). Any species observed during a RVT are then assigned a score based on what time they were first observed, allowing for a measure of relative abundance to be estimated. In effect, the RVT substitutes time for area during a search, while assuming that the most abundant species will be observed early in a trial. The RVT has been criticized for overestimating the abundance of evenly distributed species, and underestimating the abundance of patchy species (DeMartini and Roberts 1982). However, the results of the RVT were significantly correlated with the results of traditional straight-line transects (Kimmel 1985, Sanderson and Solonsky 1986), and the RVT was found to successfully characterize fish assemblages for the purpose of comparison (Sanderson and Solonsky 1986).

The original RVT of Jones and Thompson (1978) was modified as follows. Nine pre-defined habitats were treated as distinct areas, like the coral reefs of the Jones and Thompson (1978) study. Since Big Clear Lake, like most temperate waterbodies, is species-depauperate relative to tropical coral reefs, the largest change required to adapt the RVT to this study was to shorten the length of a trial. As Big Clear Lake was thought to contain approximately one-tenth the number of species found by Jones and Thompson (1978), I used a five minute duration period per trial, as opposed to the original fifty minute trials. Species were then assigned scores based on what minute they were first observed. For example, a species seen in the first minute would be assessed five points, and a species first observed in the fifth minute would be assigned one point. This scoring system is analogous to the original RVT method, where a species observed in the first ten

46

minutes of the fifty minute trial received five points, and a species first observed in the

last ten minute period would receive one point (Jones and Thompson 1978). Where

possible, fish were identified to life stage as well as species (Table 3.1).

Preliminary trials were used to determine the number of replicate trials required at

each site. Greater than 90% of the species life stages were observed with four replicate

trials (Figure 3.2), so this was the number of within-site replicates used.

For this study, a habitat classification scheme was developed based on depth,

substrate, and percent emergent cover (Table 3.2). The result was five habitat types

located in shallow water (0 - 2 m), three at mid-depths (2 - 5 m), and one in deeper water

(5 - 7 m). At mid-depths, the muddy and rocky sites found in shallower water

disappeared, whereas all vegetation except the colonial algae *Chara* spp. stopped

growing at a depth of 5 m. A few initial trials were attempted deeper than 7 m, but no

fish were ever observed. Percent cover estimates were based on the amount of

submerged macrophyte cover available, and determined by calculating the percent

macrophyte cover in a 1 m^2 quadrat. In Big Clear Lake, the dominant aquatic

macrophytes are *Potamogetan* spp. and Eurasian watermilfoil, *Myriophyllum spicatum*.

Chara spp. provided some level of cover, and because it grows in extensive monotypic

mats in Big Clear Lake, it was considered a separate habitat type.

RVT trials were conducted from June 15 to August 21, 1999 in 401 sites

distributed throughout the lake. Due to the spatially random nature of a RVT trial,

specific sites could never be re-sampled, so each RVT was treated as spatially

independent. Shallow habitats were assessed with snorkeling, whereas SCUBA was used

Table 3.1. Body length criteria used for classifying species life stages observed by RVT

(based on Scott and Crossman 1973).

Species	Length (mm)		
	YOY	juvenile	adult
northern pike (*Esox lucius*)	< 150	151-299	> 300
blackchin shiner (*Notropis heterodon*)	-	< 30[a]	> 30
mimic shiner (*Notropis volucellus*)	-	< 30[a]	> 30
bluntnose minnow *Pimephales notatus*	-	< 35[a]	> 35
golden shiner (*Notemigonus chrysoleucas*)	-	< 50[a]	> 50
brown bullhead (*Ameiurus nebulosus*)	-	< 50[a]	> 200
banded killifish (*Fundulus diaphanus*)	-	< 40[a]	> 40
pumpkinseed (*Lepomis gibbosus*)	< 30	31-109	> 110
bluegill (*Lepomis macrochirus*)	< 30	31-119	> 120
smallmouth bass (*Micropterus dolomieui*)	< 45	46-249	> 250
largemouth bass (*Micropterus salmoides*)	< 50	49-249	> 250
rock bass (*Ambloplites rupestris*)	< 40	41-199	> 200
yellow perch (*Perca flavescens*)	< 40	41-139	> 140
walleye (*Stizostedion vitreum*)	< 180	181-299	> 300
northern logperch (*Percina caprodes*)	-	< 35[a]	> 35

[a] YOY not separated from older juveniles, either because this could not be done easily by

underwater observation or because no YOY were observed.

48
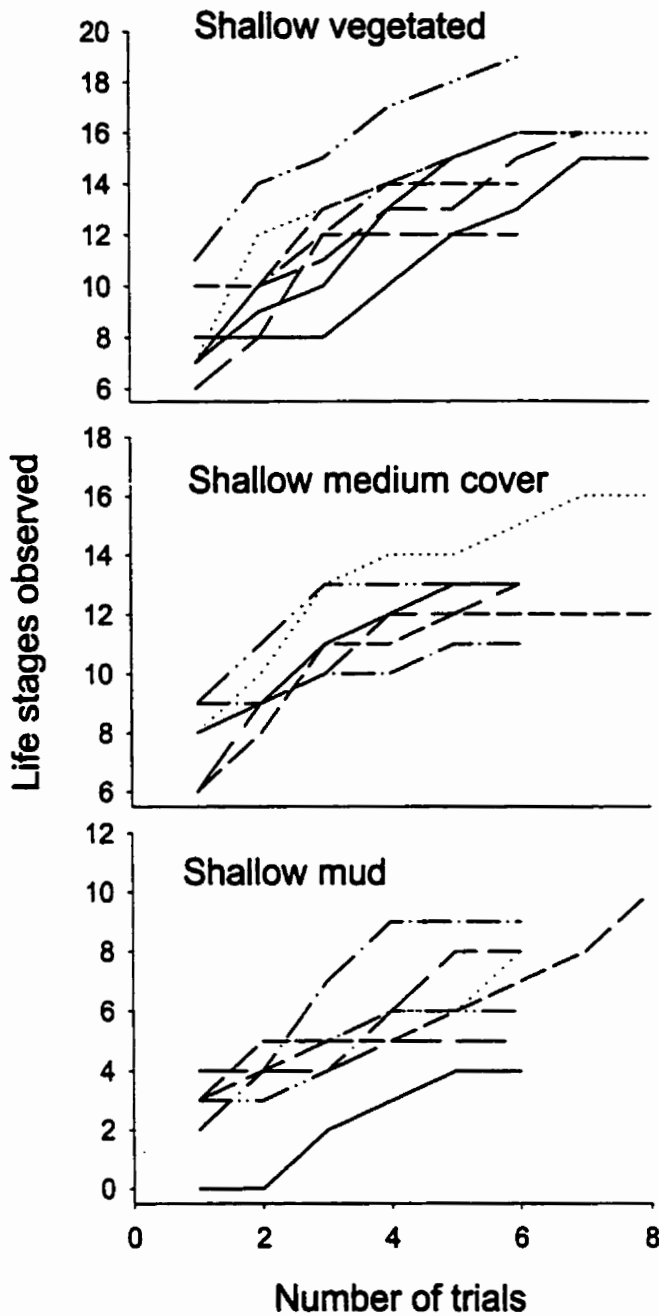
Figure 3.2. Relationship between the number of RVT trials undertaken and number of species life stages observed. Each line represents the cumulative number of species life stages observed from an individual site during successive trials. Criteria for the three habitat types presented here are defined in Table 3.2, and were selected to represent the range of available cover.

Table 3.2. Habitat classification scheme developed to separate habitats into discrete

entities. Habitats are categorized based on depth, substrate, and percent emergent cover.

Depth (m)	Substrate/cover				
	Rock	Bare	*Chara/Najas*	15% cover	> 30% cover
0-2	SR (shallow rocky)	SMu (shallow mud)	SC (shallow *Chara*)	SMi (shallow medium cover)	SV (shallow vegetated)
2-5	-	-	MC (medium depth *Chara*)	MMi (medium depth medium cover)	MV (medium depth vegetated)
5-7	-	-	DC (deep *Chara*)	-	-

for all mid-depth and deep trials. Observers were equipped with a water-resistant watch, and the time at which all species life stages were observed was recorded on a white PVC wrist slate. At each site, four replicate 5-min RVT's were performed. The scores from these replicate counts were averaged, giving a single RVT score for each site. Habitat types were sampled in approximate proportion to their availability, and the order of temporal sampling was randomized. The total number of trials performed in a given habitat type ranged from 41 - 50.

In order to assess YOY walleye prey composition, 10 individuals were captured with seines every two weeks, starting July 15, for stomach content analysis. Prior to this date, I was unable to capture YOY walleye. The first YOY walleye observation was on June 15, and as YOY walleye become piscivorous shortly after becoming demersal (Raney and Lachner 1942), it was assumed walleye were eating piscine prey in this one month period when they could be observed but not captured. Collected walleye were then taken back to the laboratory, where prey were removed from the stomachs. Identifiable prey were classified to species life stage, and their length was measured. The lengths of partially digested prey that could not be identified were determined by comparing the remaining body parts to those of a prey item of known length.

Assessment of YOY Walleye Habitat Preference and Species Associations

Walleye abundance scores obtained from RVT trials were used to assess YOY walleye habitat preferences and predator and prey associations. As most fishes undergo a series of ontogenetic shifts (Werner and Hall 1988), I first examined the data for evidence of temporal habitat shifts. Such a shift was apparent after the first four weeks of the

51

study, and this was confirmed by statistical analysis (see Results). As a result, the study period was divided into early (June 15 - July 11) and late (July 15 - August 21) demersal phases, and all hypotheses were tested in each phase.

To assess whether walleye exhibited any habitat preferences, walleye abundance scores in the nine habitat types were compared with the Kruskal-Wallis one-way Analysis of Variance. Non-parametric tests were used in all analyses involving the walleye abundance scores because of their non-normal distribution. When significant differences in habitat use were found, a Dunn's post-hoc test was performed to determine which habitats differed.

Shifts in YOY walleye distribution were also examined by comparing their spatial distribution at two levels of vegetation and depth in the early and late demersal periods. For this analysis, habitats with little or no YOY walleye utilization were excluded, and walleye abundance scores in the remaining habitats were compared with Mann-Whitney U tests. Changes in depth and vegetation usage by YOY walleye over the two time periods were examined by performing a two-way ANOVA on ranked walleye abundance data.

RVT scores for all observed species life stages were compared against YOY walleye RVT scores from the same sites to determine whether YOY walleye were positively or negatively associated with any particular species life stages. RVT scores were divided into the early (n = 127 sites) and late (n = 274 sites) demersal period, and Spearman rank correlations were then used to test for species associations.

Assessment of Prey Availability and Predation Risk on YOY Walleye Habitat Selection

Associations between sites and habitats selected by YOY walleye and the abundance of their prey and predators were examined by first developing indices of potential prey and predators, and then using these indices to assess these associations. The Prey Abundance Index (PREYIND) was based on YOY walleye stomach content data obtained from this study, supplemented by YOY walleye prey data from Raney and Lachner (1942). For the early demersal period, PREYIND was defined as the sum of the RVT scores for the following species life stages: blackchin shiner YOY, banded killifish YOY, bluntnose minnow YOY, golden shiner YOY, *Lepomis* spp. YOY, largemouth bass YOY, mimic shiner YOY and adults, yellow perch YOY, and unidentifiable fry. For the late demersal period, PREYIND was identical to that of the early period except that blackchin shiner adults were added to the prey list. Blackchin shiner adults were too large to be eaten by YOY walleye in the early demersal period.

The Predator Abundance Index (PREDIND) was developed similarly, using potential YOY walleye predators for both the early and late demersal periods in separate indices. Only species defined as active piscivores by Scott and Crossman (1973) and large enough to consume YOY walleye during the early demersal period, based on a prey to predator length ratio of 0.4 (Juanes 1994), were included in the analysis. For the early demersal period PREDIND was defined as the sum of the RVT scores for all yearling and older northern pike, largemouth bass, smallmouth bass, yellow perch and walleye. Due to rapid YOY walleye growth, a number of species life stages were no longer capable of consuming young walleye in the late demersal period based on the prey to predator length ratio of 0.4. The remaining species life stages used to compose PREDIND in the late

demersal period were yearling and older northern pike, adult largemouth and smallmouth bass, and adult walleye.

Spearman rank correlations between the prey or predator indices and the YOY walleye RVT scores were used to test the strength of predator and prey associations across habitats. YOY walleye scores were correlated with the sum of both potential prey (PREYIND) and potential predators (PREDIND) for both the early (127 sites) and late (274 sites) demersal periods. In order to determine whether the distribution of YOY walleye could potentially be explained by differences in prey availability or predation risk among habitat types, Kruskal-Wallis analyses of variance were performed to compare PREYIND and PREDIND among habitat types. Finally, PREYIND and PREDIND were used to compare the role of relative prey availability and predation risk on microhabitat selection within the most frequented habitats. To accomplish this, Student t-tests were used to compare PREYIND and PREDIND from sites where YOY walleye were observed to those from sites in the same habitat type where YOY walleye were not observed.

Assessment of YOY Walleye Shoaling Behaviour

Whenever a YOY walleye was observed during an RVT trial, the species and number of individuals shoaling (a shoal is defined as a group of fishes that remains together for social reasons (Pitcher 1986) with YOY walleye were recorded. Differences in shoaling behaviour between the early and late demersal periods were examined by comparing the average shoal size and the number of YOY walleye in each shoal. Both tests were performed on $\log_e$-transformed data with Student t-tests. Species associations

54

were also compared across time periods by determining the number of times YOY walleye were observed schooling with a particular species during each time period, and using Fisher's exact test to determine differences in species shoaling with YOY walleye across time periods.

3.3. Results

Habitat Use

There was a significant shift in YOY walleye habitat utilization patterns between the periods denoted as early demersal and late demersal (Table 3.3). This shift is evident from the change in relative usage of the various habitats in the two time periods (Figure 3.3).

Both time periods showed significant differences among habitats in their use by YOY walleye (early demersal: $H_8 = 20.2$, P = 0.01; late demersal: $H_8 = 41.2$, P < 0.001). During the early demersal period, YOY walleye primarily utilized heavily vegetated habitats at medium depths (Figure 3.3a). Four other habitats were used at intermediate levels during the early demersal period, but the remaining four habitats were rarely or never utilized. During the late demersal period, shallow *Chara* and shallow habitats with moderate cover showed the highest levels of use, and there were four habitat types in which YOY walleye were not observed (Figure 3.3b).

In general, YOY walleye appeared to move away from mid-depth, high cover habitats towards shallow, low cover habitats as they grew older and larger (Figure 3.4). While the differences in use of low and high cover areas in the early and late demersal periods were not significant (Mann-Whitney U-test, P = 0.15 and 0.16, respectively), a

55

Table 3.3. Results of a two-way ANOVA on the ranked RVT scores investigating potential shifts in YOY walleye habitat use between the early and late demersal periods.

source of variation	df	F	P
period	1	1.2	0.29
habitat	8	3.2	0.001
period * habitat	8	4.6	< 0.001
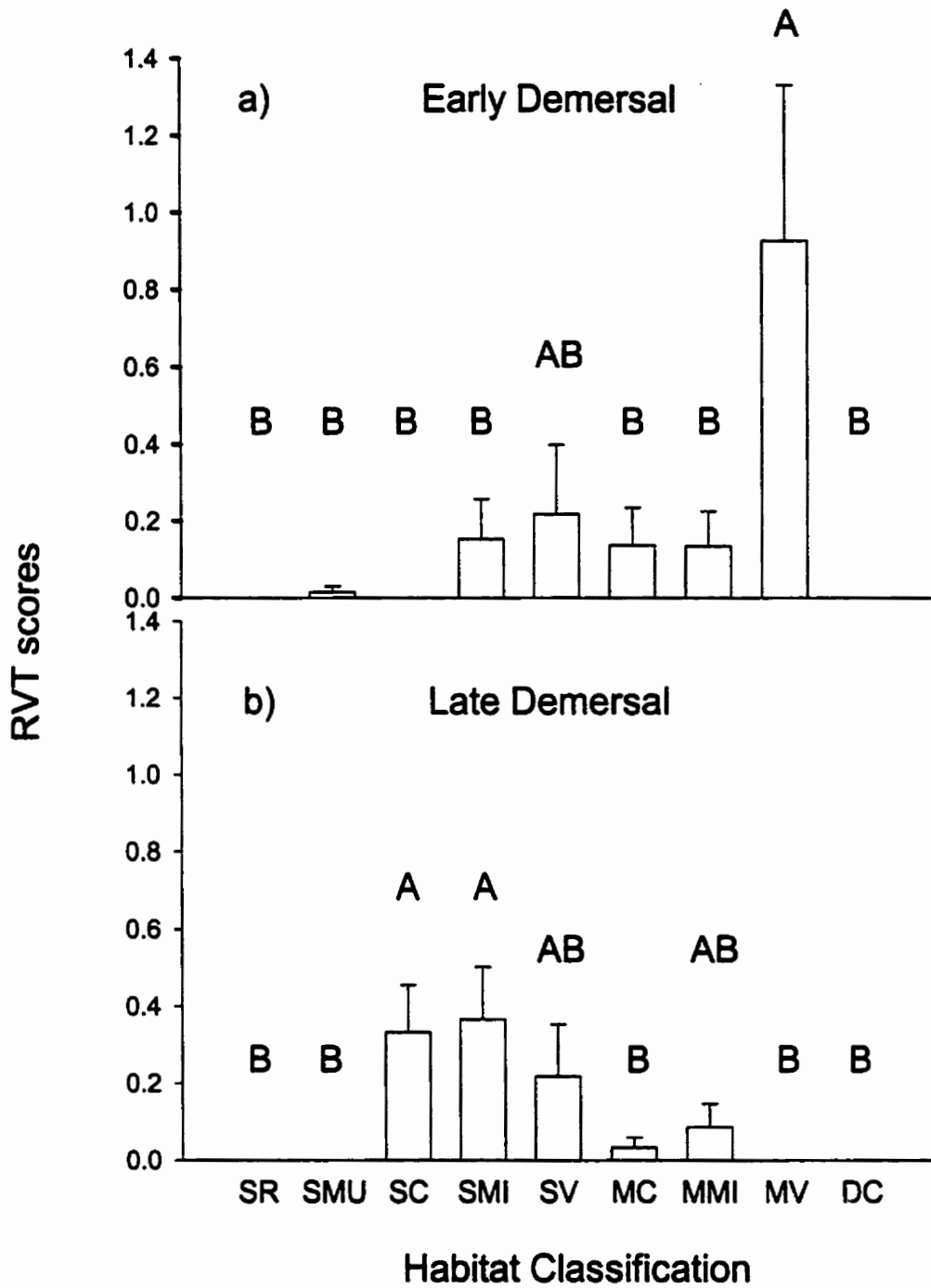
Figure 3.3. YOY habitat use in (a) the early demersal and (b) late demersal periods, as indicated by RVT scores in nine habitat types. Error bars represent SE. Means with the same letter are not significantly different. See Table 3.2 for habitat codes.
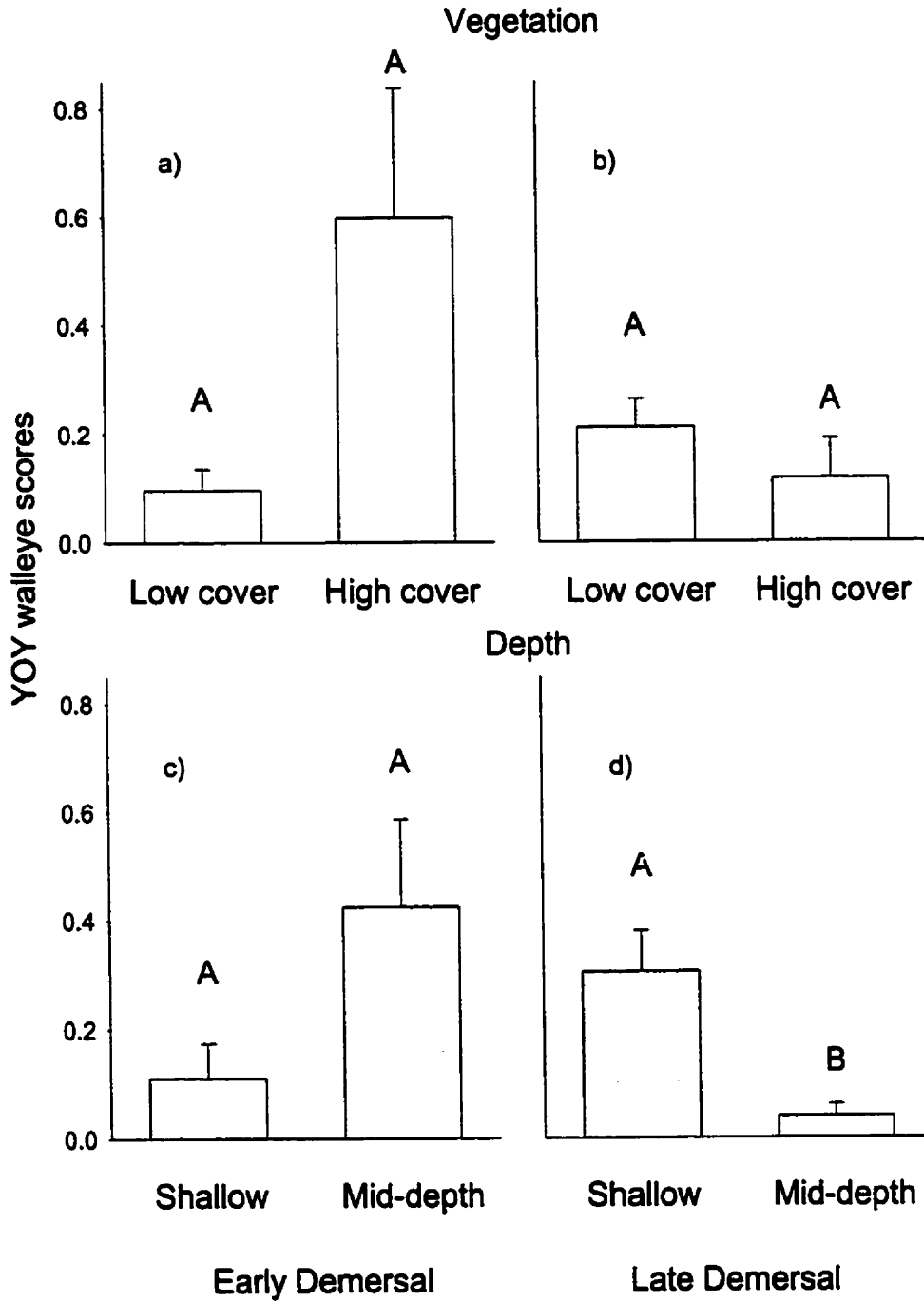
Figure 3.4. Comparison of YOY walleye RVT scores by (a, b) vegetation cover, and (c, d) depth during the early and late demersal period. Error bars represent SE. Means with the same letter or not significantly different.

significant time by cover interaction indicated there was a shift in cover utilization between the two periods (Table 3.4). A similar shift in depth distribution between the two periods also occurred (Table 3.4). Significantly more YOY walleye were observed in shallow sites than in mid-depth sites during the late demersal period (Mann-Whitney U-test, P = 0.04), whereas no significant difference in depth utilization was found in the early demersal period (P = 0.22).

Prey and Predator Associations

Stomach content analysis indicated that YOY walleye were almost entirely piscivorous by the end of the early demersal period (Table 3.5). Unfortunately, only a few of the walleye collected during this period contained identifiable prey items in their stomachs. Most of these were YOY fishes, although an adult cyprinid was also taken. The unidentifiable fishes were also mostly YOY.

Twenty-seven YOY walleye were collected in the late demersal period, and the stomach contents of the 21 which contained prey items consisted entirely of fish. The most common prey types were sunfish YOY, but five other species were identified, including an adult mimic shiner.

YOY walleye RVT score showed a significant, positive correlation with the RVT scores of three species life stages during the early demersal period, and six species life stages during the late demersal period (Table 3.6). Based on stomach content data, the three species associated with YOY walleye during the early demersal period (bluntnose minnow YOY, mimic shiner adult and yellow perch YOY) were all potential prey items, despite the fact that yellow perch YOY and mimic shiner adults were often seen in loose

59

Table 3.4. Results of a two-way ANOVA on the ranked RVT scores investigating

potential shifts in YOY walleye use of vegetation and depth between the early and late

demersal periods.

source of variation	df	F	P
Vegetation			
period	1	3.0	0.09
vegetation	1	0.5	0.50
period * vegetation	1	10.4	0.001
Depth			
period	1	0.7	0.41
depth	1	0.1	0.83
period * depth	1	12.8	< 0.001

Table 3.5. Stomach contents of YOY walleye captured in Big Clear Lake during the

summer of 1999.

Prey type	Total number of prey type found	Percentage of walleye with prey type	Mean percent volume
Early Demersal Period (n = 10 walleye; mean length = 77 mm ± 2.4 SE)[a]			
mimic shiner adult	1	10	11
bluntnose minnow YOY	1	10	3
Lepomis spp. YOY	2	20	13
Unidentified fish remains	8	60	71
Chironomid larvae	1	10	2
Late Demersal Period (n = 27 walleye; mean length = 106 mm ± 2.7 SE)[b]			
mimic shiner adult	1	4	2
mimic shiner YOY	3	4	1
bluntnose minnow YOY	4	7	4
banded killifish YOY	1	4	2
Lepomis spp. YOY	13	22	20
logperch	1	4	1
yellow perch YOY	5	15	9
unidentified fish remains	32	53	61

[a] Total number of walleye examined in early demersal period include 2 with empty

stomachs. Mean length of fish prey in the early demersal period: 11.9 mm ± 0.8 SE;

[b] Total number of walleye examined in late demersal period include 6 with empty

stomachs. Mean length of fish prey in the late demersal period; late demersal period:

19.3 mm ± 1.2 SE.

Table 3.6. Spearman rank correlations between YOY walleye RVT scores and those of other species life stages. Starred probabilities are significant after applying Bonferroni corrections.

Species	Life stage	Early Demersal (N=127)		Late Demersal (N=274)	
		r_s	P	r_s	P
northern pike	adult	- 0.07	0.46	- 0.06	0.37
	juvenile	-	-	- 0.04	0.53
blackchin shiner	adult	-	-	- 0.08	0.17
	YOY	-	-	- 0.02	0.75
mimic shiner	adult	0.30	< 0.001*	0.12	0.04
	YOY	-	-	- 0.09	0.12
bluntnose minnow	adult	0.25	0.005	0.24	< 0.001*
	YOY	0.28	< 0.001*	- 0.03	0.58
golden shiner	adult	- 0.04	0.66	0.37	< 0.001*
	YOY	-	-	- 0.001	0.98
brown bullhead	adult	0.10	0.26	- 0.07	0.29
	YOY	- 0.03	0.72	-	-
banded killifish	adult	- 0.09	0.32	0.04	0.51
	YOY	-	-	- 0.04	0.48
pumpkinseed	adult	0.09	0.31	0.20	0.001*
	juvenile	0.07	0.42	0.24	< 0.0001*
bluegill	adult	0.07	0.45	0.03	0.64
	juvenile	0.14	0.11	0.16	0.006
Lepomis spp.	YOY	0.16	0.08	- 0.11	0.08
smallmouth bass	adult	- 0.16	0.08	- 0.11	0.07
	juvenile	- 0.15	0.10	- 0.09	0.14
	YOY	- 0.12	0.17	- 0.11	0.06
largemouth bass	adult	0.05	0.58	0.04	0.52
	juvenile	0.11	0.20	0.23	< 0.0001*
	YOY	0.10	0.27	0.08	0.17
rock bass	adult	0.02	0.82	0.06	0.36
	juvenile	0.02	0.80	- 0.06	0.36
yellow perch	adult	- 0.04	0.70	0.19	0.002
	juvenile	0.08	0.37	0.18	0.003
	YOY	0.27	0.002*	- 0.05	0.38
walleye	adult	0.09	0.31	- 0.05	0.44
	yearling	0.01	0.94	0.27	< 0.0001*
logperch	adult	- 0.03	0.74	- 0.12	0.06
	YOY	- 0.08	0.37	- 0.15	0.01

shoals with YOY walleye at this time. In the late demersal period, none of the species

life stages significantly associated with YOY walleye (bluntnose minnow adults, golden

shiner adults, largemouth bass juveniles, juvenile pumpkinseeds older than age 1, adult

pumpkinseeds, and walleye yearlings) were considered potential predators or prey items.

YOY walleye were observed shoaling with most of these species (particularly the adult

golden shiners). The within habitat RVT scores for all species life stages found to be

significantly correlated with YOY walleye RVT scores are presented in Table 3.7. The

relative abundance patterns of most of these species life stages were similar to the YOY

walleye relative abundance patterns, although YOY walleye were typically less abundant

overall. A significant correlation was found between the YOY walleye RVT score at a

site and its Prey Abundance Index score during the early demersal period ($r_s = 0.36$, n =

127, P < 0.001), but not during the late demersal period ($r_s = -0.057$, n = 274, P = 0.35).

When prey availability was examined by habitat, it was found that medium and

deep habitats had significantly greater prey abundance than four of the five shallow

habitats in both the early and late demersal periods (early demersal: $H_8 = 25.6$, P < 0.001;

late demersal: $H_8 = 37.5$, P < 0.001). YOY walleye were, for the most part, found in

habitats with high prey abundance during the early demersal period (Figure 3.5a). Both

the Prey Abundance Index and the YOY walleye RVT score were highest in mid-depth

vegetated habitats, and second highest in shallow vegetated habitats. This association

disappeared during the late demersal period (Figure 3.5b), as the habitats used most

frequently had among the lowest prey availability.

When the habitat types most frequented by YOY walleye were examined

individually, it was found that prey abundance was consistently higher in sites where

Table 3.7. Within habitat RVT scores of YOY walleye and the species determined to be significantly associated with YOY walleye (from Table 3.6) in both the a) early and b) late demersal periods. Habitat codes can be found in Table 3.2.

	Habitat								
	SR	SMu	SC	SMi	SV	MC	MMi	MV	DC
a) early demersal									
walleye YOY	0	0.01	0	0.15	0.22	0.14	0.19	0.93	0
	-	(0.01)	-	(0.10)	(0.18)	(0.10)	(0.09)	(0.41)	-
mimic shiner adult	0.35	0	0.80	1.5	2.25	1.09	1.26	2.90	1.33
	(0.20)	-	(0.23)	(0.48)	(0.46)	(0.31)	(0.32)	(0.40)	(0.47)
bluntnose minnow YOY	0.2	0.02	0.44	0.25	0.63	0.55	0.24	0.40	1.79
	(0.14)	(0.02)	(0.28)	(0.18)	(0.29)	(0.41)	(0.17)	(0.21)	(0.42)
yellow perch YOY	0.44	0.75	0.56	0.91	1.48	2.06	2.21	2.23	2.17
	(0.25)	(0.26)	(0.30)	(0.34)	(0.47)	(0.48)	(0.40)	(0.37)	(0.50)
b) late demersal									
walleye YOY	0	0	0.33	0.37	0.22	0.03	0.09	0	0
	-	-	(0.12)	(0.14)	(0.13)	(0.03)	(0.06)	-	-
bluntnose minnow adult	0.61	0.18	2.08	2.24	1.40	1.99	1.45	1.46	1.44
	(0.15)	(0.06)	(0.24)	(0.22)	(0.23)	(0.23)	(0.22)	(0.26)	(0.26)
golden shiner adult	0.02	0	1.11	1.20	0.99	0.03	0.06	0	0
	(0.02)	-	(0.26)	(0.26)	(0.22)	(0.03)	(0.05)	-	-
largemouth bass juvenile	0.25	0.02	1.03	1.82	0.84	0.79	0.87	1.58	0.85
	(0.09)	(0.02)	(0.22)	(0.26)	(0.17)	(0.17)	(0.18)	(0.26)	(0.18)
pumpkinseed adult	0.93	0.42	1.67	1.86	1.92	2.10	1.64	1.82	2.10
	(0.14)	(0.15)	(0.25)	(0.21)	(0.21)	(0.23)	(0.29)	(0.26)	(0.24)
pumkinseed juvenile	2.83	0.17	3.24	3.64	3.26	2.95	2.87	2.96	2.54
	(0.22)	(0.07)	(0.30)	(0.18)	(0.27)	(0.24)	(0.23)	(0.25)	(0.25)
walleye yearling	0	0	0.42	0.2	0	0.45	0.25	0.12	0
	-	-	(0.14)	(0.1)	-	(0.15)	(0.13)	(0.05)	-
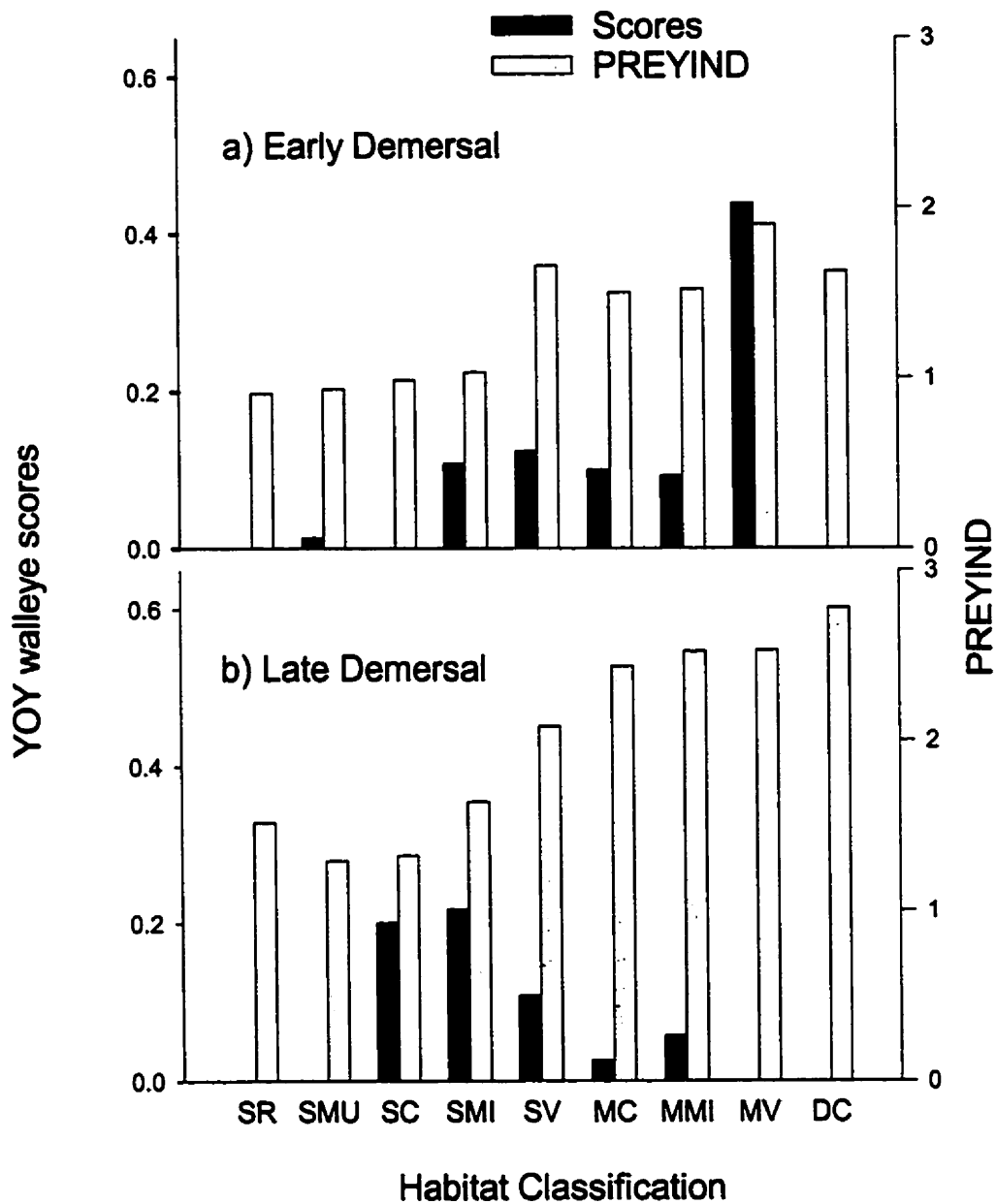
Figure 3.5. Comparison of YOY walleye habitat use patterns and prey abundance (as

indicated by the Prey Abundance Index) in the nine habitat types defined in this study in

(a) the early, and (b) late demersal periods. See Table 3.2 for habitat codes.

65

walleye were observed than in sites where they were not observed (Table 3.8). In particular, vegetated sites at medium depths (preferred during the early demersal period) and shallow sites with moderate cover (preferred during the late demersal period) with YOY walleye had significantly higher PREYIND scores than sites of the same habitat type where YOY walleye were not found. This trend was also apparent in shallow *Chara* habitats, though the difference between sites with and without YOY walleye was not significant.

YOY walleye RVT scores were negatively associated with those of a number of potential predators, but no significant relationships were observed (Table 3.8). Contrary to my prediction, the walleye RVT score at a site was not significantly correlated with its Predator Abundance Index during the early ($r_s = 0.02$, n = 127, P = 0.78) or late ($r_s = 0.02$, n = 274, P = 0.73) demersal periods.

During the early demersal period, the Predator Abundance Index was significantly lower in shallow, muddy habitats than in the other eight habitat types ($H_8 = 42.4$, P < 0.001), but YOY walleye were rarely found in these muddy sites (Figure 3.6a). In the late demersal period, the Predator Abundance Index scores also differed significantly among habitat types ($H_8 = 43.1$, P < 0.001), with vegetated habitats at medium depth generally more numerous in predators than shallow habitats (Figure 3.6b). When the three habitats most frequented by YOY walleye were examined individually, it was found that sites where YOY walleye were found did not differ significantly in predator abundance from sites where they were not found (Table 3.8).

Table 3.8. Comparison of (a) Prey Abundance (PREYIND) and (b) Predator Abundance (PREDIND) between sites where YOY walleye were found and those where they were not found. Comparisons were made in habitats most frequented by YOY walleye. See Table 3.2 for habitat codes. Values in parentheses are SE of index scores.

Period	Habitat	walleye present	walleye absent	t	df	P
a) Prey Abundance						
Early demersal	MV	8.5 (2.5)	4.4 (3.7)	2.7	13	0.01*
Late demersal	SMI	6.1 (2.8)	3.6 (1.5)	2.4	28	0.01*
Late demersal	SC	4.0 (1.8)	2.8 (1.4)	1.4	31	0.09
b) Predator abundance						
Early demersal	MV	6.6 (2.8)	6.5 (7.2)	0.03	13	0.48
Late demersal	SMI	0.5 (0.06)	0.8 (0.17)	1.4	28	0.09
Late demersal	SC	0.3 (0.07)	0.3 (0.12)	0.3	31	0.41
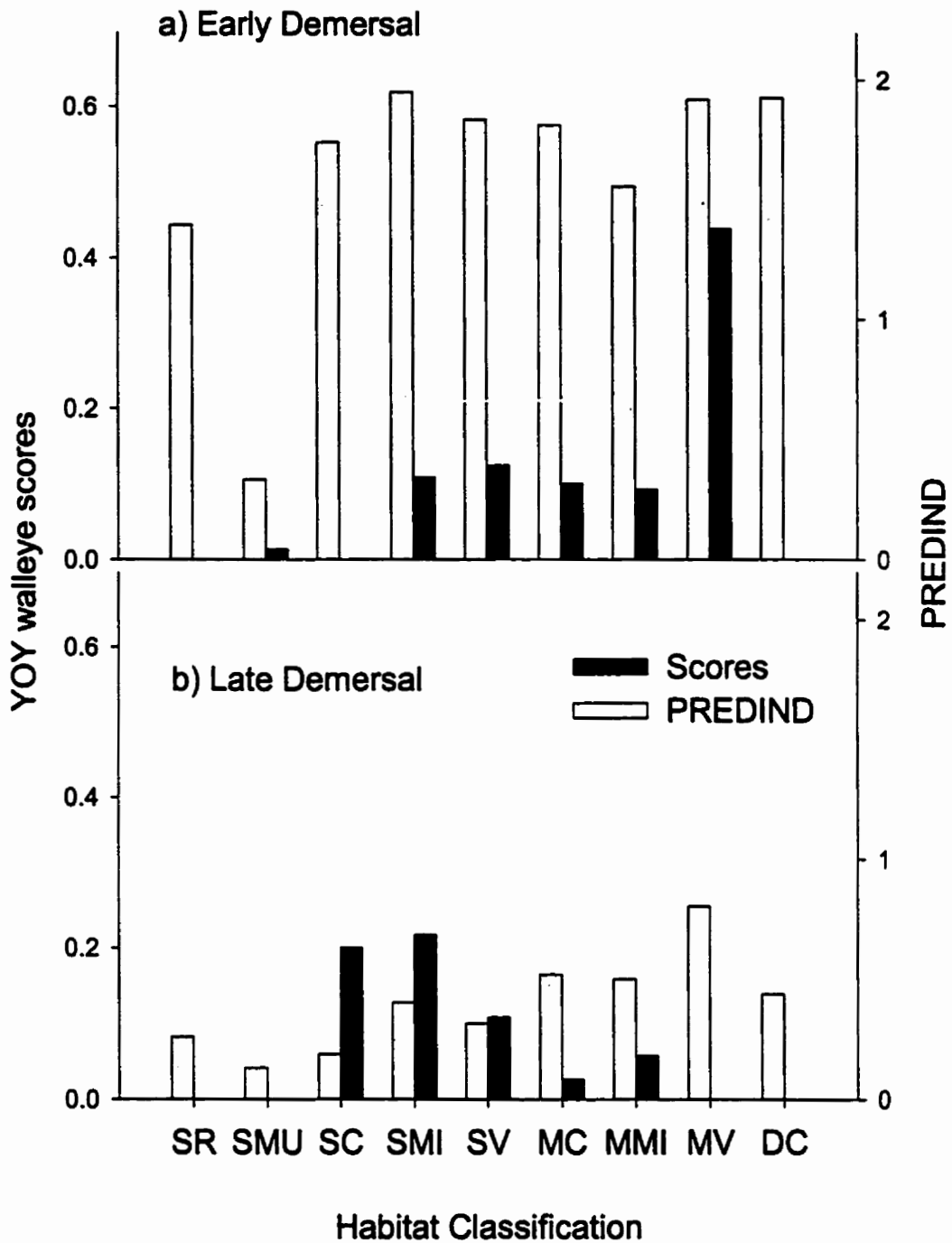
Figure 3.6. Comparison of YOY walleye habitat use patterns and predator abundance (as indicated by the Predator Abundance Index) in the nine habitat types defined in this study in (a) the early, and (b) late demersal periods. See Table 3.2 for habitat codes.

There were significant differences between the early and late demersal period in the size of shoals containing YOY walleye, the number of YOY walleye shoaling together, and the species composition of the shoals (Table 3.9). YOY walleye were associated with larger, mixed species shoals in the early demersal period, but later, they tended to shoal in smaller, more homogeneous groups. Species associations within the shoals also shifted between periods, as YOY yellow perch were commonly found shoaling with walleye during the early demersal period, but not during the late demersal period. Adult golden shiners exhibited the reverse trend, appearing in shoals with YOY walleye primarily in the late demersal period. Only adult mimic shiners were consistently shoaling with young walleye in both time periods.

3.4. Discussion

The results of this study suggest that although biotic and abiotic factors play a role in determining the distribution of young-of-year walleye in Big Clear Lake, the relative importance of physical habitat features and biotic interactions differed temporally. For the first few weeks of the demersal stage, the distribution of YOY walleye was positively related to prey availability, and walleye were found most frequently in sites of moderate depth and moderate to dense macrophyte cover. A positive relationship between the abundance of YOY walleye and their prey was predicted, as a similar relationship was noted in an Ontario river system (Leis and Fox 1996). The loss of a significant association with prey in the late demersal period was unexpected, as high prey levels were found to be associated with YOY walleye at least through the end of July by Leis

Table 3.9. Shoaling behaviour of YOY walleye in the early and late demersal period, as determined by shoal size, the number of YOY walleye shoaling together, and species associated with YOY walleye in the shoals. Shoal size and YOY abundance data are $\log_e$ - (x+1) transformed. Probabilities were determined by paired t-tests for shoal size and abundance data, and Fisher's exact tests for individual species shoaling data.

Parameter	Early Demersal (N=22)	Late Demersal (N=25)	Probability
Shoal size (± SE)	4.06 (0.30)	2.76 (0.22)	< 0.001*
Number of YOY walleye in shoal (± SE)	1.18 (0.15)	1.69 (0.15)	0.01*
Number of YOY walleye-only shoals	1	9	0.012*
Number of times seen shoaling with YOY walleye			
adult mimic shiner	11	7	0.14
adult golden shiner	2	10	0.02*
adult bluntnose minnow	3	3	1.0
bluegill juvenile	1	2	1.0
largemouth bass YOY	1	0	0.47
yellow perch YOY	7	0	0.003*
yellow perch juvenile	1	1	1.0
walleye yearling	0	1	1.0

and Fox (1996). Predator densities appeared to be unrelated to YOY walleye distribution at any time during the study. Possible explanations for the shifting balance between prey associations and habitat preference in YOY walleye habitat selection, and the apparent lack of influence of predation risk, are considered below.

Early demersal period

The early demersal period extended from mid-June until mid-July, and at this time YOY walleye were located primarily in heavily vegetated sites 2 - 5 m in depth. These sites consisted mostly of thick stands of Eurasian watermilfoil, with one or two individual walleye mixed in shoals along with hundreds of adult mimic shiners and YOY yellow perch. During this period, YOY walleye were rarely found in habitats that provided little or no cover. The utilization of heavily vegetated habitats was opposite to my predictions, as previous research has suggested that young walleye prefer more open habitats (Savoie 1983, Ritchie and Colby 1988, Lane et al. 1996), and should avoid vegetation to reduce the threat of largemouth bass predation (Santucci and Wahl 1993). It is possible that previous researchers who classified YOY walleye as habitat generalists may have missed the short time period where young walleye utilized high cover areas, as it occurred immediately after the pelagic phase and the fish were residing in areas difficult to sample using most traditional sampling gear. Raney and Lachner (1942) reported difficulty sampling YOY walleye in Oneida Lake, which were found almost exclusively in shallow macrophyte beds in first week of August. Although the timing of this observation falls outside of my definition of the early demersal period, the growth rates of YOY walleye in Oneida Lake were slower than those observed in this study, and

the fish were similar in size to those found in vegetated habitats in Big Clear Lake. This suggests the timing of the YOY walleye habitat shifts may be size, rather than age-dependent.

The apparent YOY walleye habitat preferences may be masking a greater dependence on prey availability during the early demersal period. As predicted, there was a significant relationship between prey availability and YOY walleye abundance. Furthermore, three prey species were significantly correlated with YOY walleye abundance across all habitats during the early demersal period. These results, in combination with the occurrence of higher prey levels in vegetated habitats, suggest the habitat preferences detected here may be prey-related.

Few studies have actually investigated the relative importance of prey and habitat associations in fishes, and the results have not been consistent. Some researchers have found strong habitat and weak prey associations (Perrow et al. 1996, Eklöv 1997, Connell and Kingsford 1998), while others have found the opposite (Leis and Fox 1996, Muotka et al. 1998). The presence of both habitat and prey associations have been found in at least one other study (Rozas and Odum 1988). Both Rozas and Odum (1988) and Eklöv (1997) focussed on species targeted by piscivores, and both studies found the strongest habitat preference and highest prey availability in vegetated areas. Their results parallel those of this study, and suggest that high prey availability may be one possibility as to why high cover habitats are preferred by YOY walleye in the early demersal period.

Though the prediction that YOY walleye would actively avoid potential predators was not supported, there was also little difference among habitats in the abundance of potential predators during the early demersal period. Thus, it is possible that the use of

high cover habitats could then have been expected, as many YOY fishes use the vegetated areas of the littoral zone to minimize the risk of predation (Werner et al. 1983b, Mittelbach 1984, Gotceitas and Colgan 1990). Fishes that face periods of high predation risk often mitigate predation pressure by selecting habitats, such as those with high macrophyte density, that reduce predator efficiency (Savino and Stein 1982, Gotceitas and Colgan 1990). The fact that high prey densities were also present in high cover areas suggests that YOY walleye may not have suffered any habitat-mediated reductions in growth, unlike most species that use structurally complex habitats to mitigate predation risk (Werner and Gilliam 1984, Mittelbach 1984).

While vegetation stands that are too dense can inhibit foraging efficiency (Gotceitas 1990), even the high cover habitats defined by this study should have been sparse enough to allow foraging while providing some refuge from potential predators. This would put YOY walleye in the beneficial position of reducing predation risk while maximizing growth, the latter being an important determinant in the eventual survival rate of most fishes (review by Sogard 1997). An early switch to piscivory (Raney and Lachner 1942, Houde and Forney 1970) allows YOY walleye to grow much faster than most other fishes, and it is likely that they are faced with high predation risk for only a short time relative to species that spend years in littoral areas before moving to open water. Wahl (1995) suggested that fast growing species may have poorly developed antipredatory behaviours because they face a narrow window of predation vulnerability, and that these behaviours may be mitigated by habitat selection. This explanation would account for the approximately three weeks that young walleye used high cover habitats. In Big Clear Lake, YOY walleye did not leave the vegetated areas until they were approximately 75 mm in length, which is large enough to substantially reduce the risk of predation once they moved to low cover habitats.

Late demersal period

Considerable changes were observed in YOY walleye habitat preferences and prey associations after July 15. YOY walleye completely abandoned the mid-depth vegetated habitat, and moved to shallower habitats with less available cover. The move to areas with reduced cover areas fits the traditional view of YOY walleye habitat selection (Savoie 1983, Ritchie and Colby 1988, Lane et al. 1996), but the selection of primarily shallow water (< 2 m depth) suggests that YOY walleye may not be as affected by high light levels as older individuals (Ryder 1977). Other studies have found YOY walleye at depths of up to 10 m by the fall (Raney and Lachner 1942), and while the intensive component of this study ended in August, periodic SCUBA observations that extended into October indicated that most YOY walleye were still in shallow, low cover habitats at that time.

The strong prey associations evident in the early demersal period had ended by the start of the late demersal period. The significant relationship between YOY walleye and prey availability disappeared, and the species that were earlier found to be strongly correlated with YOY walleye changed from potential prey to non-prey species of similar size that shoaled with the walleye. As previously noted, the loss of a strong prey association was unexpected because the strong prey association found in the Montreal River extended through the month of July (Leis and Fox 1996). One possible explanation is the difference between the two systems in productivity and prey availability, with Big Clear Lake being the more productive of the two systems. The combination of higher latitude and lower productivity in the Montreal River may have kept YOY walleye tied to their prey for a longer period in that system, and the shorter duration of the Leis and Fox

74

(1996) study meant that YOY walleye may not have been sampled during the period when prey become less important. It is interesting to note that, despite the lack of a significant association between the abundance of YOY walleye and their prey in the late demersal period, walleye did occupy sites within preferred habitat types that had a higher abundance of prey. This suggests that YOY walleye may still be using prey availability as a secondary site selection mechanism in the late demersal period.

The rapid growth of YOY walleye in Big Clear Lake continued through the late demersal period, as by early August YOY walleye had reached approximately 120 mm in total length. At that size, the number of potential predators would be greatly reduced. The absence of a negative correlation between the relative abundance of YOY walleye and that of their potential predators would suggest that predator avoidance was not a major factor in site selection by YOY walleye in the late demersal period. This result was suprising given the observed YOY walleye habitat selection, as the use of shallow water as a refuge from piscivores has been observed in a number of fishes (Power 1984, Matthews et al. 1986, Schlosser 1988, Angermeier 1992, Ruiz et al. 1993, Eklov et al. 1994). One possible explanation for such results is that the PREDIND used in the above analysis was too broad, and that specific predators influence the distribution of YOY walleye more than others. In particular, the use of shallow habitats by YOY walleye in the late demersal period could be a response to avoid cannibalism by older walleye, which has been suggested as the major factor determining walleye year class strength in some lakes (Chevalier 1973, Forney 1976). Adult walleye were observed on only a single occasion in shallow habitats during the late demersal period. However, adult walleye forage most actively at night (Ryder 1977), while the quantitative component of this

study occurred during daylight hours. While the results suggest that neither predator avoidance or prey availability can satisfactorily explain the distribution of YOY walleye during the late demersal period, the ecological literature suggests predator avoidance would more likely explain the observed selection of shallow water habitats at this time.

YOY walleye shoaling behaviour

YOY walleye group size decreased significantly between the early and late demersal periods, lending further credence to the suggestion that the selection of highly vegetated habitats during the early demersal period is at least partially due to predator avoidance. Large shoaling groups, like those observed during the early demersal period, help decrease the vulnerability of individuals to predation (Pitcher 1986). The average group size that YOY walleye were associated with during the early demersal period was over 100 individuals, but that number fell to less than 10 individuals by the late demersal period. Similar group size and habitat relationships were noted with comparable size classes of yellow perch, a close relative of walleye (Eklöv 1997). In that study, small perch (< 80 mm) were located in areas of intermediate vegetation density and found in groups of greater than 10 individuals, while large perch (> 110 mm) were located in areas with less cover in groups of less than 10 individuals (Eklöv 1997).

YOY walleye tended to shoal with increasingly large fishes as they grew; initially with YOY yellow perch, and later with adult mimic shiners, adult golden shiners, and by the end of the study, with other YOY walleye. Such size- and species-sorting within fish shoals is expected, as phenotypic homogeneity is an important characteristic of group formation (Ranta et al. 1994, Krause et al. 1996). By early July the YOY walleye were

76

larger than YOY yellow perch and adult mimic shiners, and were preying on them even as they shoaled together. Walleye are capable of consuming prey half their own length (Campbell 1998), and by shoaling with potential prey during the early demersal period, YOY walleye likely benefit by increasing their predator detection and foraging abilities (Clark and Mangel 1986).

One observation from this study that should be examined in more detail in the future was the apparent stability of YOY walleye shoals in the late demersal period. Groups were consistently located in the same sites, and the number of individuals in these groups remained fairly constant. Some behavioural work has been conducted on group structure and dynamics in yellow perch (Helfman 1984), which were determined to be facultative shoalers. It would be interesting to follow the initial walleye shoals observed here over a few years to determine whether groups remained associated over time, as similar sized groups of yearlings and adults were frequently observed in Big Clear Lake. Such site-specific associations would also make the outcome of any lethal sampling programs on smaller waterbodies problematic, as new groups would be unlikely to move into previously sampled areas.

Other considerations

The specific microhabitat and species association data gathered by this study could not have been collected without using an underwater visual technique, as traditional sampling gear such as seines, gillnets or electrofishers would have been unable to sample such a diverse fish fauna as effectively (Hayes 1983, Hubert 1983), or provide the resolution necessary (Sale 1980). Visual methods are not perfect sampling tools

77

(Brock 1982, Helfman 1983), but given the changes YOY walleye undergo in their first year, it was decided that visual techniques were most likely to provide answers to the questions posed in this study. Alternate techniques for sampling YOY walleye were tried, including small-mesh gillnets and straight-line underwater visual transects (Chapter 2). For this study, the rapid visual technique (RVT) was chosen as the technique most likely to effectively sample YOY walleye. While the RVT has been criticized on grounds that the scoring system underestimates spatially clustered species and overestimates widespread but rare species (DeMartini and Roberts 1982), the use of the RVT in this study was not specifically to estimate all species abundances, but rather to focus on one species. Therefore, if any sampling biases were introduced, they should be consistent across habitat types. If anything, the distribution of YOY walleye would likely be underestimated using the RVT, as they are spatially clumped and their distribution would likely represent a negative binomial distribution (DeMartini and Roberts 1982).

During the early demersal period, YOY walleye inhabited high cover areas and were found in large shoals, while during the late demersal period these fish were located primarily in shallow water areas. These behaviours are suggestive of prey fishes using mechanisms to reduce the probability of being consumed, yet my index of predation risk was found to be unimportant for either the early or late demersal period. Thus, it is possible that the importance of diel habitat shifts, a potentially confounding factor not quantifiably investigated by this research, may be influencing the prey and predator indices used here. In particular, older walleye are more active at night (Ryder 1977), and cannibalism can greatly influence walleye year-class strength (Chevalier 1973, Forney 1976). Other potential predators present in Big Clear Lake are also known to forage

78

nocturnally, including smallmouth bass (*Micropterus dolomueui*) and brown bullhead (*Ameuris nebulosus*) (Scott and Crossman 1973). Therefore, habitat-specific predation risk may vary over the diel period, and the non-significant influence of predators during daylight hours may not be reflective of predation risk during the crepuscular and overnight periods. Species included in the PREYIND are not as likely to be affected by this problem, as they are typically active during the day. In the months of June and July, some effort was made to assess the nocturnal activity of YOY walleye by returning to observe fish that were observed earlier in the day. These fish were difficult to relocate, but in the two instances where YOY walleye were observed at night, the fish were resting near the substrate and not active. However, adult walleye were often observed moving through shallow areas at night, and these fish were presumably foraging. Thus, future research should address the potential for different patterns in prey and predator abundance between diurnal and nocturnal periods.

In conclusion, the YOY walleye habitat utilization patterns observed in this study were unexpected, as previous studies had indicated YOY walleye were habitat generalists (review by Kerr et al. 1997). The relationship between YOY walleye and their prey during the early demersal period was predicted, though the shift away from strong prey associations during the late demersal period was not (Leis and Fox 1996). The results indicate moderate prey and habitat associations in areas of heavy vegetation for the early demersal period, and then an abrupt shift to shallower, low cover habitats and away from strong prey associations. The early habitat selection and shoaling behaviour of YOY walleye suggests young walleye are likely influenced by potential predators, and their behaviour (inhabiting areas of high macrophyte density and living in large shoals) is

typical of many other prey species living under the threat of predation. It was also apparent, though, that YOY walleye likely passed this vulnerable period quickly with their rapid growth. Thus, this research suggests that YOY walleye are sensitive to the risk of predation for a short period during their early life history, and that they reside in habitats capable of maximizing growth and reducing predation by residing in refuge areas during this critical period.

The shifting patterns of walleye prey and habitat associations detected by this research are important in understanding the early life history of this species. The relationships observed here will hopefully provide the background necessary to further investigate the causal factors involved in YOY walleye habitat selection, in particular the separation of prey and habitat associations during the early demersal period.

Chapter 4.

The Influence of Predation Risk on the Overwinter Mortality and Energetic Relationships of Young-of-the-Year Walleye (*Stizostedion vitreum*)

4.1. Introduction

Size-dependent processes are known to strongly influence recruitment patterns in temperate YOY fishes. The survival of young fishes is frequently size-dependent (Werner and Gilliam 1984), where small differences in growth can lead to large differences in survival (Houde 1987). Smaller members of a cohort can face higher mortality, either through size-selective predation, size-dependent physiological processes, environmental processes that selectively remove smaller individuals (e.g. oxygen or temperature extremes), or size-dependent susceptibility to pathogens (review by Sogard 1997). One period when size-dependent processes are important in determining the ultimate survival of many temperate young-of-year (YOY) fishes is the first overwinter period (Shuter and Post 1990). Research on a number of species has shown that the rate of overwinter survival is lower for smaller individuals in a YOY cohort (e.g. Chevalier 1973, Forney 1976, Toneys and Coble 1979, Shuter et al. 1980, Post and Evans 1989a, Johnson and Evans 1991, Bernard and Fox 1997), although size-dependent overwinter survival in temperate fishes is not pervasive (Toneys and Coble 1979, Madenjian et al. 1996).

Size-dependent overwinter mortality in fishes can occur for physiological reasons. Cold water temperatures lead to reduced, or a complete cessation of, feeding in some species, and as YOY fish have lower absolute energy reserves and higher weight-specific

81

metabolic rates (Paloheimo and Dickie 1966), they have to subsist primarily off their own diminishing lipid and protein reserves. Shuter and Post (1990) suggested that, after the larval life stage, the first overwinter period is the stage at which temperate fishes are most susceptible to starvation. In some species, such as smallmouth bass (*Micropterus dolomieui*), there is an established relationship between smaller body size and lower energy stores (Oliver et al. 1979, Shuter et al. 1980). However, the young of coolwater species, such as walleye (*Stizostedion vitreum*), may not face the same physiological challenges as other temperate freshwater fish, as they are capable of feeding at lower temperatures (Galligan 1960, Kelso 1972).

For species that can feed during overwinter periods, higher size-specific metabolism is not the only possible factor that would lead to size-dependent mortality. Size-specific predation could also contribute to smaller individuals being selectively removed from the population. This has been documented for walleye in Oneida Lake, where adult walleyes were selectively preying upon the smaller individuals of YOY walleye cohorts, indicating that cannibalism may lead to size-dependent mortality (Chevalier 1973). Size-selective predation was also used to explain overwinter mortality patterns in Lake Mendota YOY walleye (Madenjian et al. 1991). Forney (1976, 1980) concluded that cannibalism was the most important factor regulating YOY walleye survival in Oneida Lake. If a cohort could reach an average length of >175 mm at the end of the first growing season, cannibalism was relatively low in that lake (Forney 1976). As such, Forney (1976) found that walleye year-classes in this lake were not formed until after the first overwinter period, suggesting that size-dependent mortality may be one factor influencing YOY walleye recruitment. Cannibalism may also limit the

effectiveness of walleye stocking programs, as stocking successive year-classes is rarely successful in Minnesota (Li et al. 1996b), perhaps due to the cannibalistic nature of age-1 walleye.

Two experiments that have evaluated YOY walleye overwinter survival in relation to body size and lipid concentrations reported similar results. Results to date suggest that size-specific metabolic costs do not lead to size-dependent mortality in YOY walleye, as the studies found high survival for all sizes of walleye (Jonas and Wahl 1998, Copeland and Carline 1998). In addition, Copeland and Carline (1998) found no influence of body size or lipid concentrations on YOY walleye survival in lakes or ponds. However, no overwinter predation experiments have been undertaken to determine whether YOY walleye cohorts are susceptible to size-selective predation, as walleye cohorts tend to be larger than the cohorts of most other temperate species.

The potential effects of size-specific metabolic costs and size-specific predation on YOY survival also fail to account for a potentially important interaction between the two that may impact survival. Fishes raised in the presence of predators experience stress reactions (Rehnberg 1987, Järvi 1989, Huuskonen and Karjalainen 1997), thereby increasing their metabolic rate. Predators could enhance the size-specific metabolic costs for the smaller individuals of a YOY cohort even if not directly consuming them, resulting in size-selective mortality in the presence of predators that would not have occurred otherwise (Miranda and Hubbard 1994a). The presence of predators may also lead to reduced overwinter energy reserves, leading to size-selective overwinter mortality in yellow perch (*Perca flavescens*), a close relative of walleye (Post and Evans 1989b). Therefore, predator intimidation, an indirect effect of predation, may also play a role in

the overwinter survival of walleye by increasing metabolic rates and more rapidly decreasing energy reserves.

The goal of this study was to determine whether larger body size was associated with greater overwinter survival in YOY walleye in both the presence and absence of predators. Based on the above literature, the following predictions were made: (1) smaller YOY will have lower pre-winter energy levels than larger YOY, and will deplete them at a higher rate; (2) despite the predicted increase in energy depletion, no size-related differences in overwinter survival are expected in the absence of predators; and (3) in the presence of predators, the added physiological stress, in combination with size-selective predation on the smaller individuals, will lead to size-selective overwinter mortality in YOY walleye.

4.2. Methods

Rearing procedures

Walleye for the study were obtained from the Ontario Ministry of Natural Resources' (OMNR) White Lake Fish Culture Station (lat. 44°48'; long. 76°47'). Eggs and sperm were obtained in the spring from Napanee River parental stock. Eggs were reared in incubation jars in the hatchery, and one or two-day old fry were transferred to fertilized outdoor rearing ponds. The young walleye remained in these ponds for approximately 2 months, at which time the ponds were drained and the walleye transferred indoors into circular rearing tanks. The fish were initially reared on a diet of

Biokiowa™, then switched to a standard trout pellet diet. Walleye were kept in the hatchery until fall, when the experiments were initiated.

Pond experiment

Experiments were conducted for three overwinter periods, from the fall of 1997 to the spring of 2000, in outdoor hatchery rearing ponds at the OMNR Westport Fish Culture Station (lat. 44°40'; long. 76°23'). The study initiation and termination dates, and average sizes of fish, varied among years, due to differences in the onset of winter and spring (Table 4.1). Prior to the transfer of fish to the Westport ponds in the fall, each fish was marked with an individual combination of dorsal spine clips. Because of differences in hatchery production, the number of walleye used in the experiments differed each year.

Four cement-bottom rearing ponds were utilized for each overwinter experiment. The ponds were all 0.3 ha, with a mean depth of 2 m, and were left dry one month prior to the commencement of each experiment to ensure that no unwanted fishes were present. The ponds were supplied with water through a parallel, gravity-fed piping system, with water originating from a natural lake adjacent to the facility. Water was constantly fed into each pond at similar rates of flow, and the constant inflow of cool water was assumed to keep oxygen levels well above the requirements of overwintering walleye. Oxygen concentrations were measured during periodic visits to the ponds, and concentrations were never < 10 mg / L. Water temperature was also measured during these visits, and temperatures ranged between 2 – 4 ° C during the overwinter period. Ponds were equipped with a stop log system, which allowed for gradual draining at the termination of

Table 4.1. Study initiation and termination dates, number of walleye used per pond, initial

mean length (±SE), initial mean weight (±SE), and initial size range of all YOY walleye

used for overwinter experiments.

Initiation date	Termination date	Number stocked (per pond)	Length (mm)		Weight (g)	
			Mean	Range	Mean	Range
09/24/97	04/10/98	40	111.1 (0.9)	81 - 146	11.3 (0.2)	5.2 - 21.8
09/26/98	04/21/99	27	105.7 (0.7)	90 - 124	9.5 (0.2)	5.7 - 15.0
09/22/99	03/30/00	75	98.2 (0.6)	73 - 146	7.6 (0.2)	3.3 - 24.7

each overwinter experiment. Pond outflows were blocked with 4 mm wire mesh to prevent emigration, while a 40 mm mesh screen served to prevent immigration of larger fishes through the inflow.

Other than the recording of water temperatures during periodic visits to the study site, individual temperature data were not collected for each pond. Climate data over the three year study period were provided from a weather station located at the Queens University Biological Station on Lake Opinicon, which is situated approximately 15 km south of the Westport Fish Culture Station. Daily air and water (from 1.2 m below the surface of Lake Opinicon) temperatures were averaged for the months of October through April. These data were then used to compare annual temperature regimes and ice formation and dissolution dates.

The study design consisted of two predator-free ponds (controls), and two ponds where predators were added. In 1997, a combination of one walleye and three burbot (*Lota lota*) were used as the predator treatment. During the 1998 trials, four burbot per pond were used as predators, while in 1999 four walleye per pond made up the predator treatment. Predatory burbot ranged in size from 25 – 40 cm, while walleye ranged in size from 30 – 35 cm. In total, there were six predator and six predator-free ponds examined through the three overwinter seasons.

Predators were added to the ponds upon initiation of the study, along with 300 YOY fishes (primarily *Lepomis spp.*) in order to provide potential prey for the walleye. Greater than 90 percent of the prey fishes were recaptured each spring, suggesting the YOY walleye were not extensively feeding during the overwinter period. All predators were recovered except in 1998-99, when only one and two burbot, respectively, were

collected out of the initial four planted in each predator pond. At the end of each experiment, ponds were slowly drained until only 0.3 m of water remained in a small cement basin in front of the screen. Ponds were then seined repeatedly until no fish were captured for 3 successive attempts. Surviving walleye were identified from their dorsal spine clips, measured (fork length in mm) weighed to the nearest 0.01 g, euthanized in an ice bath, and frozen in water for later energetic analysis (1999-2000 fish only).

Analysis of body composition

The body composition of individual walleye were determined by calculating the percent lipid, percent protein, percent water, and specific energy content of surviving fish against dry weight from the 1999-2000 trials, plus 20 pre-winter hatchery fish from across the full size range. The specific energy content was calculated by assigning lipids a value of 39 $kJ \cdot g^{-1}$ and protein 24 $kJ \cdot g^{-1}$; both on a dry weight basis (Jobling 1995, Berg and Bremset 1998). Individual fish were thawed, homogenized in a coffee grinder, and the entire sample (or subsample for larger fish) placed in an aluminum foil dish. Samples were dried in a drying oven at 90° C for at least 48 hours, until stable weights were obtained. Pre-weighed foil dishes containing dried, homogenized fish were then placed in a dessicator for 12 hours and weighed to the nearest 0.001 g. The entire dried sample was then ground to a fine powder using a mortar and pestle, and transferred to a pre-weighed Whatman cellulose extraction thimble.

Fat content was determined in a Soxhelet apparatus, using a solvent of petroleum ether (Dobush et al. 1985). Each cellulose extraction thimble and its associated homogenized fish was refluxed for 6 hrs. For larger fish, two or three samples were

analyzed to allow a comparison of within-fish variability. The thimbles were allowed to dry, placed in an oven at 90° C for 24 hours and in the dessicator for 12 hours, and then reweighed, yielding the lipid-free dry weight. Lipids were expressed as percent dry weight. As carbohydrates typically make up < 2 percent body weight in fishes (Craig 1977, Jonsson et al. 1997), protein mass was determined as the weight difference between the fat-free samples and the ash remaining after combustion (Berg and Bremset 1998). Samples were ashed for 24 hours at 550 ° C in the extraction thimble; the extraction thimble completely disappeared during the ashing process.

Data analysis

The marking of individual fish allowed for size-specific individual survival and weight change to be determined over three overwinter periods. The effect of the predator treatment on the overwinter survival of YOY walleye was determined by arcsine-transforming the percent survival in each pond [$p' = $ arcsine ($\sqrt{p}$)], and converting the result to radians (Zar 1999). These transformed data were then used in a two-way analysis of variance (ANOVA) to determine whether survival differences existed between walleye exposed to a predator treatment and those reared in a predator-free environment. All statistical analyses were considered significant at $P \leq 0.05$.

The effect of body size on individual survival was examined by dividing the walleye into four quartiles, based on pre-winter weight from each pond. Survival differences among weight quartiles were compared by performing a maximum likelihood chi-square test on every pond from each overwinter experiment. The Yates correction

factor was used in all cases, as the degree of freedom for all tests was equal to three (Zar 1999).

The effect of predators on the body condition of YOY walleye was determined by comparing the length-weight regressions for each treatment. Lengths and weights for all analyses were $\log_e$-transformed to normalize the data. The resulting regression slopes were analyzed for treatment differences using an ANCOVA. Differences in body condition between pre- and post-winter YOY walleye were also compared using an ANCOVA to determine whether the length-weight regression changed overwinter.

The relationship between $\log_e$-transformed pre-winter body length on the post-winter weight, absolute dry lipid, percent dry lipid, absolute dry protein, percent dry protein, percent water, and total energy content of individual fish were compared between predator and predator-free treatments for the 1999-2000 overwinter periods using analyses of covariance (ANCOVA's), where the covariate was $\log_e$-transformed pre-winter length. A third group, walleye sacrificed prior to the onset of winter, was added to the analysis in order to provide baseline (pre-winter) data.

To initially estimate the change in overwinter wet body weight, the two replicate ponds for each treatment were analyzed for differences using a nested ANOVA, testing for differences between replicates by nesting replicate ponds within treatments across years. No replicate differences were found, but significant differences among years meant an ANCOVA had to be performed separately for each trial year. Pre-winter length was not a significant covariate for any year, so the data were re-analysed to test for treatment effects using one-way ANOVA's.

For body composition variables, the two replicate ponds from the 1999-2000 study were tested for within-treatment differences using a Student's t-test in order to ensure there were no pond effects. When no differences were detected, individual fish were used to determine differences in body composition parameters between walleye sacrificed pre-winter, fish exposed to predation risk, and fish reared in predator-free ponds.

Initial body composition analyses involved comparing the predator treatments for absolute differences in $\log_e$-transformed lipid and $\log_e$-transformed protein dry weight using ANCOVA's. The total dry lipid and protein mass were used to test for differences among treatments, using $\log_e$-transformed pre-winter length as the covariate.

The specific energy content was calculated for each fish using untransformed dry lipid and protein weights, and the resulting data were $\log_e$-transformed. Among treatment differences were compared with ANCOVA, using $\log_e$-transformed pre-winter length as the covariate.

Differences in relative body composition were determined among treatments by initially testing for differences in the percent water content using ANCOVA, with $\log_e$-transformed pre-winter length as the covariate. As body size was found to significantly influence water content, ANCOVA analyses were performed on the percent $\log_e$-transformed dry lipid and protein (as opposed to using wet weights). As pre-winter length was determined to be a non-significant covariate for the percent dry lipid data, the data were re-analyzed using a one-way ANOVA. When significant treatment effects were detected, Tukey post-hoc comparison tests were used to separate groups.

4.3. Results

Climate data

Ice formation on Lake Opinicon occurred as early as November 30, 1997, while in 1998 and 1999, the ice formed approximately three weeks later (December 23 and 19, respectively). Winter ice cover disappeared by March 26 in 2000, the earliest ice out on record at the Queens University Biological Station, and on April 6 and 11 in 1998 and 1999, respectively. This meant the total days of ice cover were 127, 109, and 98 days in 1997-98, 1998-99, and 1999-2000, respectively.

Overall, there was little variation in mean water or air temperatures among the three overwinter periods (Figure 4.1). In all three years, mean monthly air temperatures at the declined until January, when it began to gradually increase. Water temperatures followed a similar pattern, and appeared to reach a stable plateau at approximately 2 ° C from December through February.

Overwinter survival, weight change, and body condition

Results from a two-way ANOVA showed there were no significant differences in the survival rate between YOY walleye reared with potential predators and those reared in predator-free environments ($F_{1,6} = 0.24$, $P = 0.65$), no yearly differences in YOY walleye survival rate ($F_{2,6} = 1.59$, $P = 0.28$), and no significant predator treatment * year interaction ($F_{2,6} = 1.99$, $P = 0.22$). However, a closer look at the data reveals that survival patterns were highly variable across years (Table 4.2). Fish reared in the presence of predators had lower survival in two of the three years, but not in 1997-98.

92
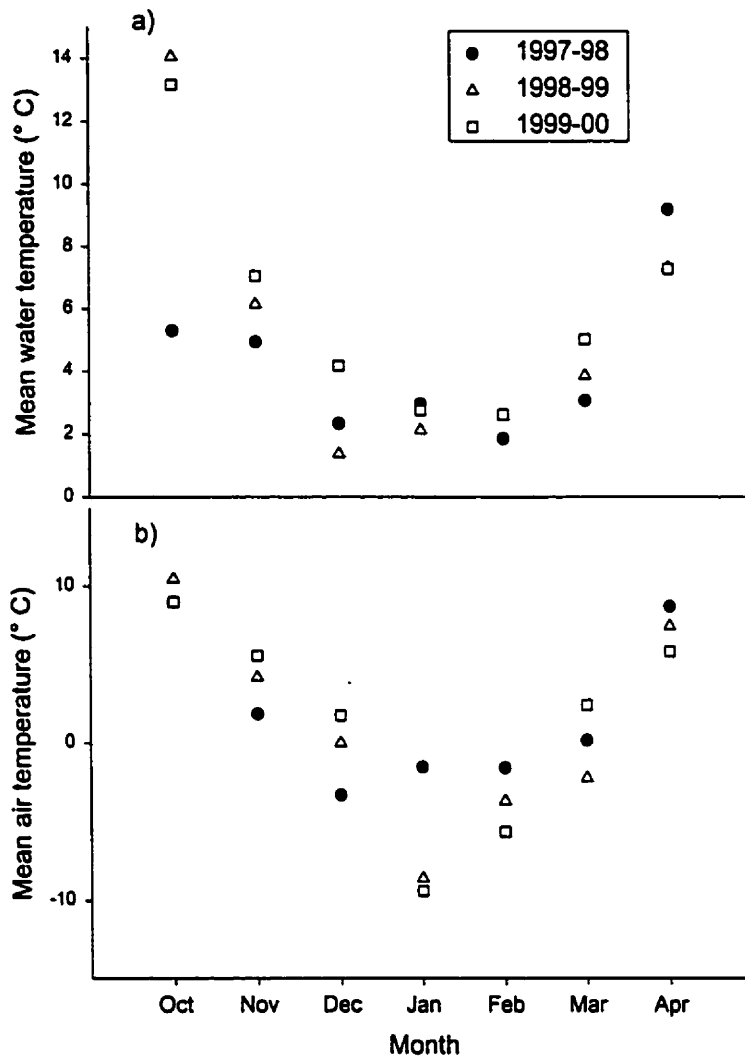
Figure 4.1. Mean a) water (from 1.2 m below surface of Lake Opinicon) and b) air

temperature data from three overwinter periods. Data were taken from a weather station

at the Queens University Biological Station.

Table 4.2. Percent survival of walleye reared in the presence and absence of potential predators from three overwinter periods, and the percent survival by treatment from all three years combined.

Year	Percent survival	
	Predator	No Predator
1997-98	49	19
1998-99	35	81
1999-00	17	22
Overall	30	33

One apparent anomaly in the data was the 81 percent survival rate observed in fish reared in the non-predator ponds during the winter of 1998-99; no other treatment had greater than 50 percent survival.

There was no evidence for size-dependent overwinter mortality in YOY walleye in any of the three years, as no significant survival differences were observed between the four weight groups from any pond regardless of treatment (Table 4.3). This suggests that the addition of predators had no effect on size-dependent mortality, which does not support my prediction that predators would selectively prey on smaller walleye.

The change in YOY walleye body weight did not differ significantly between replicates within years, but significant differences were found among years (Table 4.4). On average, YOY walleye lost weight over the 1997-98 overwinter period, gained weight in 1999-2000, and had similar pre- and post-winter weights in 1998-99. Thus, weight change data were pooled by predator treatment within years and analyzed for treatment differences using pre-winter body length as a covariate for each study period (raw data in Appendix 4.1). ANCOVA analyses revealed that pre-winter length was a significant covariate only for the 1999-2000 overwinter period (Table 4.5, Figure 4.2). Thus, the data from 1997-98 and 1998-99 were re-analyzed with one-way ANOVA's. The 1998-99 data showed no treatment effects, though the influence of predators was nearly significant ($F_{1,62}$ = 3.7; P = 0.06). Co-habiting with a predator led to significantly reduced body weights in YOY walleye in both 1997-98 and 1998-99 (1997-98 $F_{1,51}$ = 6.1; P = 0.02; 1999-2000 $F_{1,53}$ = 34.5; P < 0.001). Walleye that overwintered with potential predators tended to experience a greater loss in body weight than walleye reared without potential predators (Figure 4.2). In 1999-2000, smaller walleye from both treatments

95

Table 4.3. Survival by weight grouping for each pond from the a) 1997-98, b) 1998-99, and c) 1999-00 overwinter experiments. Walleye from each pond were divided into quartiles by weight, and survival compared across weight groups using maximum likelihood χ^2 analysis. The mean weight and percent survival are provided for each quartile within ponds, while χ^2 results are presented for each pond.

a) 1997-98

Weight quartile	Predator ponds (n = 40 / pond)				Predator-free ponds (n = 40 / pond)			
	Pond 1		Pond 2		Pond 1		Pond 2	
	$\chi^2 = 0.5$; P = 0.93		$\chi^2 = 1.1$; P = 0.71		$\chi^2 = 6.6$; P = 0.09		$\chi^2 = 1.7$; P = 0.65	
	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival
Q1	7.9 (0.3)	20	7.8 (0.4)	80	7.9 (0.5)	30	7.3 (0.4)	10
Q2	10.2 (0.2)	20	10.1 (0.1)	90	10.3 (0.2)	0	9.7 (0.2)	10
Q3	12.4 (0.2)	10	12.1 (0.3)	70	12.2 (0.2)	30	11.6 (0.1)	20
Q4	14.4 (0.3)	20	15.8 (0.5)	80	16.2 (0.7)	50	15.1 (0.9)	0

b) 1998-99

Weight quartile	Predator ponds (n = 29 / pond)				Predator-free ponds (n = 29 / pond)			
	Pond 1		Pond 2		Pond 1		Pond 2	
	$\chi^2 = 0.8$; P = 0.86		$\chi^2 = 0.4$; P = 0.94		$\chi^2 = 5.0$; P = 0.17		$\chi^2 = 4.8$; P = 0.19	
	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival
Q1	7.3 (0.1)	13	7.4 (0.3)	63	7.9 (0.3)	100	6.8 (0.2)	50
Q2	8.0 (0.1)	0	8.9 (0.1)	71	9.2 (0.2)	57	8.4 (0.2)	71
Q3	9.5 (0.2)	0	10.2 (0.2)	71	10.6 (0.1)	86	9.9 (0.2)	86
Q4	12.6 (0.5)	0	12.2 (0.3)	57	11.7 (0.2)	100	12.6 (0.6)	100

Table 4.3 continued

c) 1999-2000

Weight quartile	Predator ponds (n = 75 / pond)				Predator-free ponds (n = 76 / pond)			
	Pond 1		Pond 2		Pond 1		Pond 2	
	$\chi^2 = 3.7; P = 0.30$		$\chi^2 = 2.0; P = 0.58$		$\chi^2 = 1.1; P = 0.78$		$\chi^2 = 1.3; P = 0.72$	
	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival	mean weight (g ± SE)	percent survival
Q1	4.7 (0.2)	5	5.5 (0.1)	16	4.9 (0.1)	26	5.4 (0.1)	16
Q2	6.2 (0.1)	11	6.7 (0.1)	21	6.2 (0.1)	37	6.3 (0.1)	5
Q3	7.6 (0.1)	11	8.5 (0.1)	16	7.5 (0.1)	42	7.4 (0.1)	5
Q4	10.5 (0.5)	28	12.4 (0.9)	33	10.2 (0.5)	32	11.6 (1.0)	11

Table 4.4. Determination of within replicate variability in the change in overwinter body weight across years. The results from a nested ANOVA are presented in a), while the mean weight change (± SE) for each pond by year is found in b). Starred probabilities indicate statistical significance.

a)	F*	df	Probability
Replicate	0.14	3, 169	0.95
Year	30.7	2, 169	<0.001*

b)
1997-98

	Predator ponds		Predator-free ponds	
	Mean weight change	n	Mean weight change	n
Pond 1	-6.54 (1.7)	7	-3.33 (0.9)	11
Pond 2	-5.41 (0.6)	32	-3.46 (2.1)	4

1998-99

	Predator ponds		Predator-free ponds	
	Mean weight change	n	Mean weight change	n
Pond 1	-2.2 (0.8)	17	0.2 (0.9)	25
Pond 2	-5.2 (-)	1	-1.0 (0.9)	22

1999-2000

	Mean weight change	n	Mean weight change	n
Pond 1	-0.5 (1.0)	10	5.4 (0.8)	27
Pond 2	-2.8 (1.4)	14	7.5 (2.2)	7

Table 4.5. The effect of pre-winter length on the overwinter change in body weight of individual YOY walleye, as determined by ANCOVA. Data are presented for three overwinter periods, and starred probabilities indicate statistical significance.

Year	Factor	Statistic	Probability
1997-98	Treatment (Predator)	$F_{1,50} = 5.8$	$P = 0.02*$
	Pre-winter length	$F_{1,50} = 0.4$	$P = 0.53$
	Treatment * Pre-winter length	$F_{1,49} = 2.7$	$P = 0.11$
1998-99	Treatment (Predator)	$F_{1,62} = 3.8$	$P = 0.06$
	Pre-winter length	$F_{1,62} = 3.1$	$P = 0.08$
	Treatment * Pre-winter length	$F_{1,61} = 4.0$	$P = 0.052$
1999-2000	Treatment (Predator)	$F_{1,53} = 34.5$	$P < 0.001*$
	Pre-winter length	$F_{1,53} = 4.7$	$P = 0.03*$
	Treatment * Pre-winter length	$F_{1,52} = 0.9$	$P = 0.34$
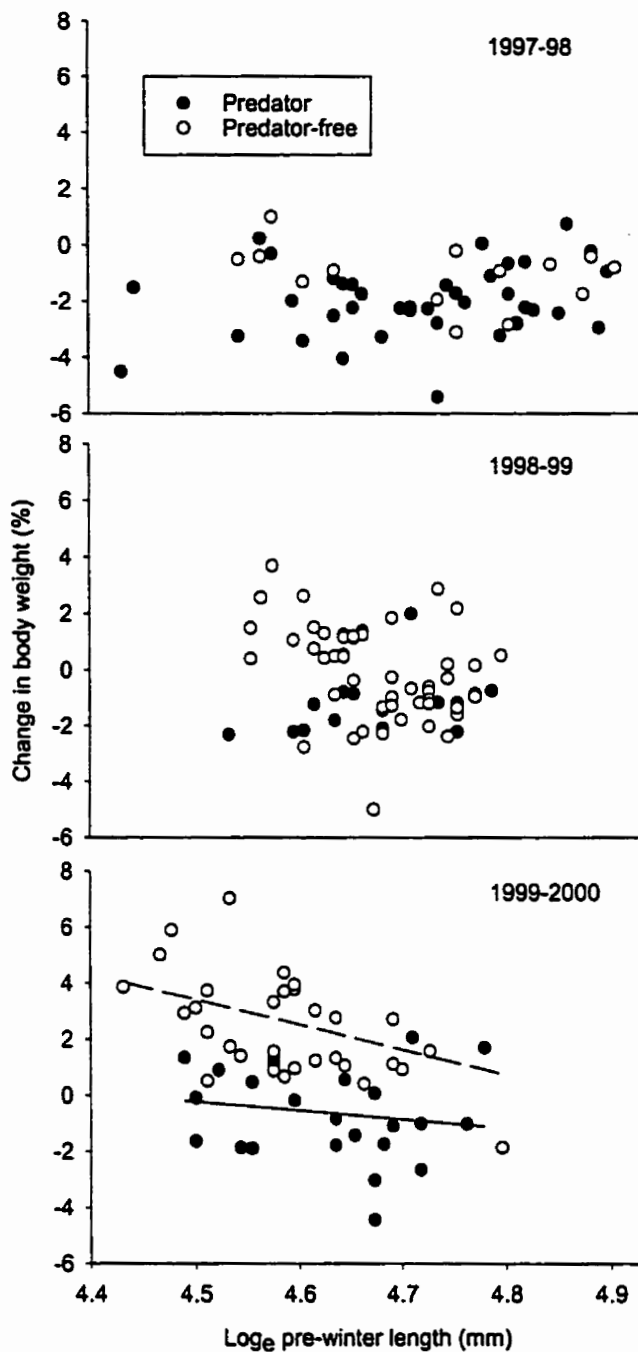
Figure 4.2. The effect of predator treatment and pre-winter length on the overwinter weight (wet weight) change of young-of-year walleye across three overwinter periods. Regression summaries and coefficients of determination from 1999-2000 are: predator exposed fish (—) $y = -3.12x + 13.80$, $n = 24$, $r^2 = 0.03$, $P = 0.45$; non-predator exposed fish (– –) $y = -8.92x + 43.56$, $n = 32$, $r^2 = 0.13$, $P = 0.04$).

100

tended to show greater weight gain than did larger walleye, which was not expected based on the premise that smaller individuals would be at a physiological disadvantage.

No difference was observed in the length-weight regressions of walleye reared in the presence and absence of potential predators (Predator treatment * covariate $F_{1,175}$ = 0.04, P = 0.95; Figure 4.3a), suggesting that body condition was similar in all walleye that survived the overwinter period. However, significant differences were found in the pre- and post-winter length-weight regressions of surviving walleye (Time treatment * covariate $F_{1,354}$ = 2508.8, P < 0.001; Figure 4.3b). This interaction appeared to be driven by a reduction in body condition in larger fish, which supports the earlier observations that larger walleye lost more weight than smaller walleye.

Lipid, protein, water, and total energy relationships

Body composition data were first analyzed to ensure within-treatment variability was low, and as no significant differences were determined between fish from replicate ponds (Table 4.6), analyses for treatment and body size (pre-winter length) effects continued using ANCOVA's. As predicted, significant treatment and body size effects were found when dry lipid mass was compared among treatments, while among treatment slopes were found not to differ significantly (Table 4.7). Predator-exposed walleye had significantly lower lipid levels than walleye reared in predator-free ponds, and this relationship was consistent across body sizes (Figure 4.4).

Significant treatment * body size interactions were detected when dry protein mass and the specific energy content were compared among treatments. Smaller fish
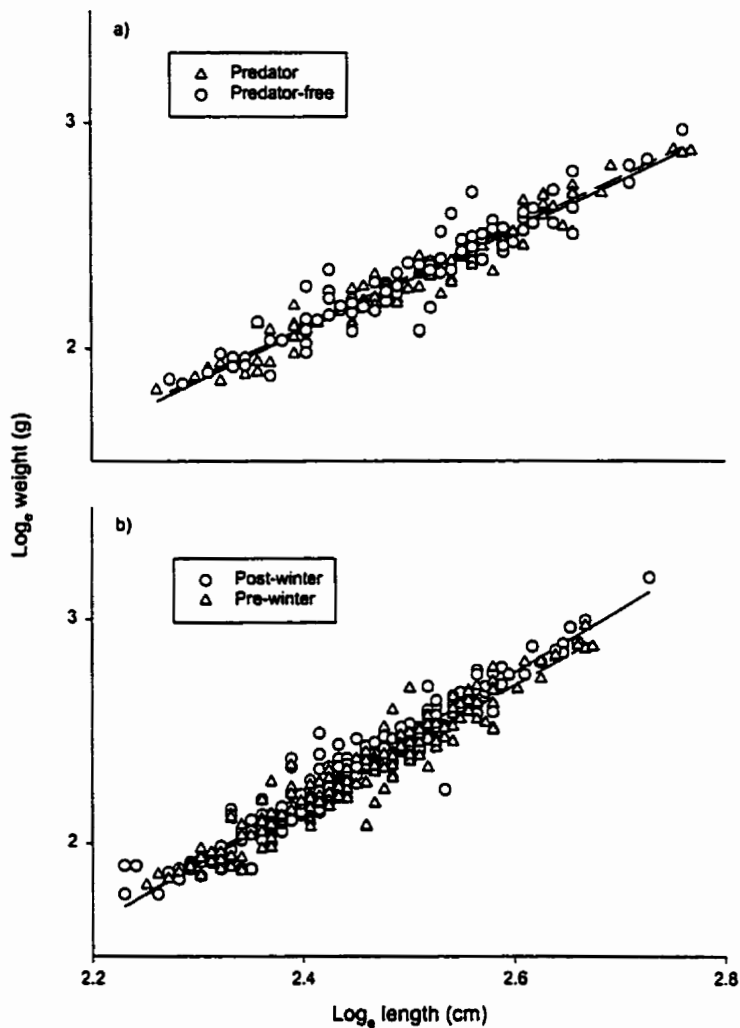
Figure 4.3. Length-weight regression for a) walleye reared overwinter in predator and
predator-free ponds (regression summaries and coefficients of determination are: predator
exposed fish (—) $y = 2.67x - 4.25$, $n = 84$, $r^2 = 0.95$, $P < 0.001$; non-predator exposed fish
(– –) $y = 2.68x - 4.25$, $n = 95$, $r^2 = 0.89$, $P < 0.001$), and b) surviving walleye from both
treatment pre- and post-winter (regression summaries and coefficients of determination
are: pre-winter (—) fish $y = 2.81x - 4.56$, $n = 179$, $r^2 = 0.94$, $P < 0.001$; post-winter fish
(– –) $y = 2.67x - 4.23$, $n = 179$, $r^2 = 0.92$, $P < 0.001$).

102

Table 4.6. Comparison of variability from ponds given the same treatment for percent dry

lipid, percent dry protein, percent water, and total energy levels from walleye reared in

the 1999-2000 overwinter period.

Parameter	Predator	Predator-free
Percent dry lipid	t = 0.60 df= 23; P = 0.56	t = 1.02; df = 32; P = 0.32
Percent dry protein	t = 0.10 df= 23; P = 0.91	t = 0.09; df = 32; P = 0.94
Percent water	t = 0.51; df= 23; P = 0.62	t = 2.00; df = 32; P = 0.054
Specific energy	t = 0.10; df= 23; P = 0.92	t = 2.02; df = 32; P = 0.052

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Table 4.7. The effect of pre-winter length and predator treatment on the body composition of YOY walleye, as determined by ANCOVA's. Data are from fish from the 1999-2000 cohort, and starred probabilities indicate statistical significance. When the treatment * covariate interaction was not significant, the term was removed and the analyses re-run.

Parameter	Factor	Statistic	Probability
Total lipid	Treatment (Predator)	$F_{2,73} = 9.0$	$P < 0.001*$
	Pre-winter length	$F_{1,73} = 28.7; r = 0.42$	$P < 0.001*$
	Treatment * Pre-winter length	$F_{2,71} = 0.60$	$P = 0.55$
Total protein	Treatment (Predator)	$F_{2,73} = 4.7$	$P = 0.012*$
	Pre-winter length	$F_{1,73} = 319; r = 0.89$	$P < 0.001*$
	Treatment * Pre-winter length	$F_{2,71} = 13.3$	$P < 0.001*$
Absolute energy content	Treatment (Predator)	$F_{2,73} = 13.1$	$P < 0.001*$
	Pre-winter length	$F_{1,73} = 282; r = 0.85$	$P < 0.001*$
	Treatment * Pre-winter length	$F_{2,71} = 9.5$	$P < 0.001*$
Percent dry lipid	Treatment (Predator)	$F_{2,73} = 5.9$	$P = 0.004*$
	Pre-winter length	$F_{1,73} = 1.2; r = 0.02$	$P = 0.24$
	Treatment * Pre-winter length	$F_{2,71} = 0.1$	$P = 0.90$
Percent dry protein	Treatment (Predator)	$F_{2,73} = 0.9$	$P = 0.43$
	Pre-winter length	$F_{1,73} = 8.5; r = 0.37$	$P = 0.005*$
	Treatment * Pre-winter length	$F_{2,71} = 1.8$	$P = 0.17$
Percent water	Treatment (Predator)	$F_{2,73} = 4.4$	$P = 0.02*$
	Pre-winter length	$F_{1,73} = 5.5; r = -0.18$	$P = 0.02*$
	Treatment * Pre-winter length	$F_{2,71} = 1.3$	$P = 0.29$
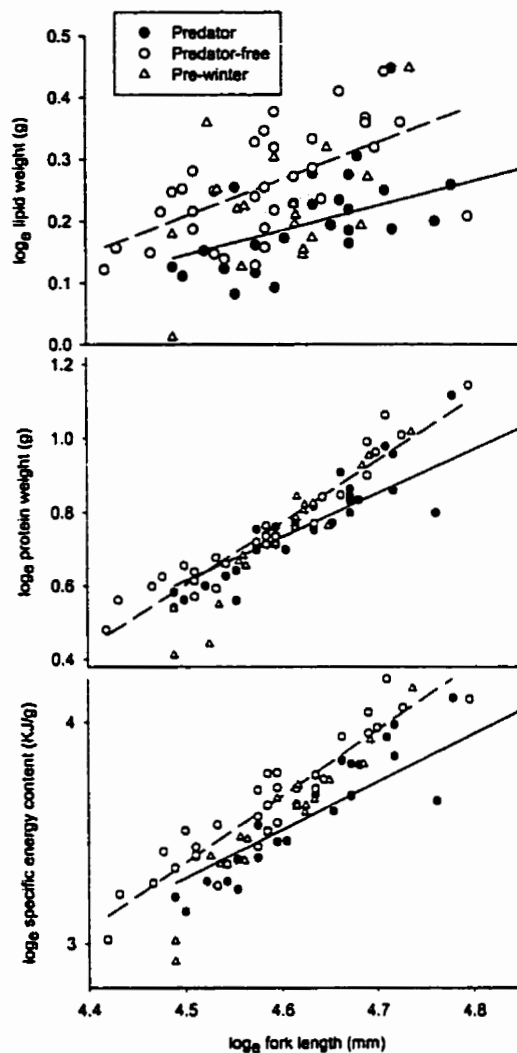
Figure 4.4. Relationship between fork length and the total lipid and protein mass in YOY walleye sacrificed pre-winter, and walleye reared overwinter in the presence and absence of predators. Lipid regression summaries: predator (—) y = 0.52 −1.7, n = 25, r^2 = 0.27, P = 0.008; predator-free (– –) y = 0.60x − 2.5, n = 34, r^2 = 0.36, P < 0.001, pre-winter (···) y = 0.46x − 2.8, n = 18, r^2 = 0.21, P = 0.055. Protein regression summaries: predator exposed (—) y = 0.86x - 4.7, n = 25, r^2 = 0.73, P < 0.001; predator-free (– –) y = 0.96x − 7.0, n = 34, r^2 = 0.92, P < 0.001, pre-winter (···) y = 0.96x − 10.1, n = 18, r^2 = 0.91, P < 0.001. Specific energy content regression summaries: predator (—) y = 0.85x − 6.5, n = 25, r^2 = 0.72, P < 0.001; predator-free (– –) y = 0.94x − 10.1, n = 34, r^2 = 0.97, P < 0.001, pre-winter (···) y = 0.96x − 15.3, n = 18, r^2 = 0.92, P < 0.001.

105

appeared to have similar protein levels among treatments, but larger walleye reared with predators seemed to have lower protein mass than either pre-winter or predator-free walleye. The significant specific energy content covariate interaction appears driven by the pre-winter fish, as the slopes of the treatment walleye raised overwinter were similar. It is apparent that the specific energy content of walleye reared overwinter in the presence of predators was lower than all but the smallest pre-winter fish (Figure 4.4). Contrary to my predictions, there was no evidence that smaller walleye depleted lipid or protein reserves faster than larger walleye.

An ANCOVA on the percent water levels of YOY walleye found that pre-winter length was a significant covariate (Figure 4.5, Table 4.7). Thus, analyses on the percent lipid and percent protein data continued using only dry weights. The presence of predators significantly affected water levels across the size range, as smaller walleye tended to have higher water concentrations, and in general predator-exposed walleye had higher concentrations than either predator-free or pre-winter fish. The size-specific water content relationship did not appear to be as strong among predator-exposed fish, but no significant differences among treatment slopes were detected.

ANCOVA analyses found that pre-winter length was only significantly related to percent dry protein (Figure 4.6, Table 4.7, raw data in Appendix 4.2). This meant that further ANCOVA analysis on the percent dry lipid data was not appropriate, so analysis for this parameter continued with a one-way ANOVA.

Predators did not significantly affect protein levels, however, as protein content was found to be similar among walleye groups. In general, larger YOY walleye had
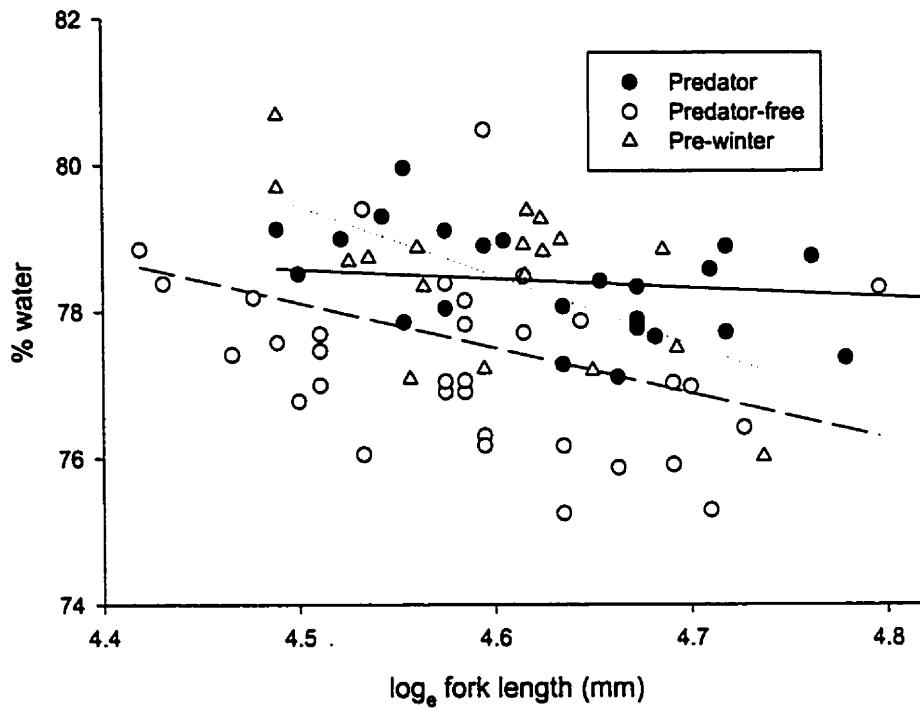
Figure 4.5. The role of pre-winter body length and predator treatment on the percent

water content (relative to wet weight) of YOY walleye reared overwinter in 1999-2000.

Percent water regression summaries and coefficients of determination are: predator

exposed (—) $y = -0.17 x + 84.2$, $n = 25$, $r^2 = 0.03$, $P = 0.40$; predator-free (– –) $y = -0.27x$

+ 105.8, $n = 34$, $r^2 = 0.07$, $P = 0.12$, pre-winter ($\cdots$) $y = -0.58x + 122.0$, $n = 18$, $r^2 = 0.34$,

$P = 0.01$.
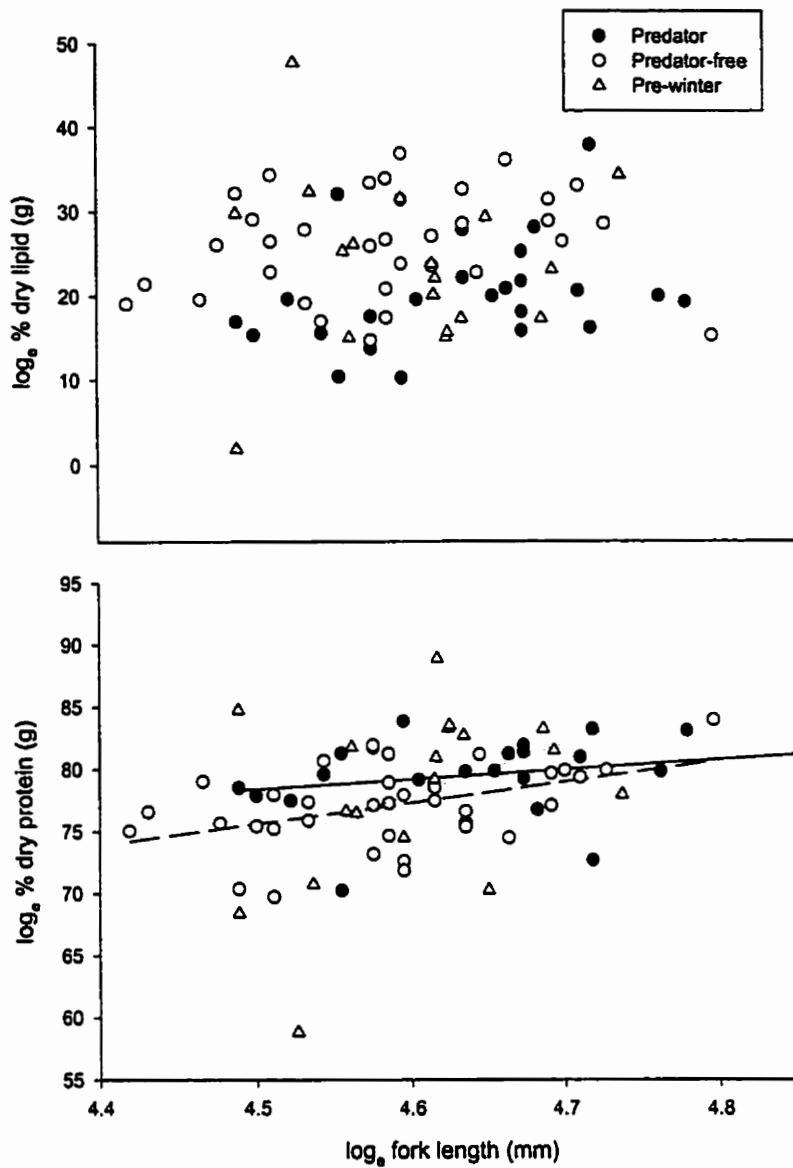
Figure 4.6. The importance of pre-winter body length and predator treatment on the

percent dry lipid and percent dry protein of YOY walleye reared overwinter in 1999-

2000. Percent dry protein regression summaries and coefficients of determination are:

predator exposed (—) y = 0.26 x + 42.6, n = 25, r^2 = 0.07, P = 0.21; predator-free (– –) y

= 0.46x – 0.95, n = 34, r^2 = 0.21, P = 0.007, pre-winter (···) y = 0.38x - 110.0, n = 18, r^2 =

0.15, P = 0.12.

higher size-specific protein levels, as predicted. Significant treatment effects were observed when the percent lipid content was compared between walleye reared with and without predators, and walleye sacrificed prior to the onset of winter ($F_{2,74} = 5.2$, $P = 0.008$). YOY walleye reared in predator ponds had significantly lower lipid levels than those reared without predators, suggesting that co-habitation with potential predators added a physiological cost. Lipid levels in pre-winter walleye were not significantly different from either treatment, and their mean lipid concentration was between the lipid levels of predator and non-predator exposed fish (Table 4.8).

4.4. Discussion

Size-selective predation

This study found no evidence for size-selective overwinter mortality in YOY walleye raised in either the presence or absence of potential predators. This lack of support for size-selective mortality in walleye is mirrored in other controlled studies where walleye were overwintered in tanks or ponds without predators (Jonas and Wahl 1998, Copeland and Carline 1998), and in empirical studies (Madenjian et al. 1996, Copeland and Carline 1998). Size-selective overwinter mortality has been observed in other natural populations, such as Lake Oneida (Chevalier 1973, Forney 1976) and Lake Mendota (Madenjian et al. 1991). In these lakes, cannibalism was believed to be the mechanism by which the smaller individuals of a YOY cohort are removed during the overwinter period.

Table 4.8. The mean percent dry lipid of YOY walleye sacrificed prior to the onset of winter, fish subjected to overwinter predator exposure, and fish reared overwinter in predator-free ponds.

Body composition parameter	Treatment		
	Predator present n = 26	Predator absent n = 34	Pre-winter n = 18
Lipid content (% ±SE)	20.2 (1.3)	26.3 (1.1)	23.8 (2.4)

The reason why size-selective mortality was not observed in this study may be due to the fact that predation was not an important source of direct mortality. No differences in overwinter mortality were observed between walleye reared in the presence or absence of predators, and as predation is typically proposed as the mechanism behind size-selective overwinter mortality in walleye populations, it may not be surprising that size-selective mortality was not detected here. Despite the presence of a large adult walleye population, the absence of size-selective overwinter mortality on Lake Erie has also been attributed to the lack of cannibalism, as an extensive survey of adult walleye stomachs indicated that cannibalism was negligible (Madenjian et al. 1996). The forage base in Lake Erie is quite different than the percid based ecosystems found in Mendota and Oneida lakes, where cannibalism occurs, as adult walleye in Lake Erie primarily forage on clupeids (Madenjian et al. 1996).

One possible explanation for the absence of size-selective predation is that the predators used in this study were not large enough to be effective predators on YOY walleye. Piscivores are constrained to certain prey sizes due to gape-limitations (e.g. Hambright 1991), and walleye can typically consume prey up to 50% of their body length (Campbell 1998). While young walleye grow more rapidly than the young of many other fishes, most of the YOY walleye used in this experiment averaged only 30% the length of predators. Thus, the burbot and walleye used as predators should have been capable of consuming almost all of the overwintering YOY walleye. However, piscivores invariably select smaller prey than predicted or than their gape will allow (review by Juanes 1994), so it is possible that the predators consumed mainly the smaller prey fishes provided as prey for the YOY walleye.

Overwinter survival

The 32% average survival rate for YOY walleye in this study was much lower than that found in the controlled overwinter studies of Jonas and Wahl (1998) and Copeland and Carline (1998), who found survival rates of 77 and 86%, respectively. A number of factors can influence the overwinter survival of juvenile fishes, including winter duration, differences in water temperature, rearing density, and pre-winter condition. Winter duration played an important role in determining the overwinter survival of yellow perch (Post and Evans 1989b), but did not appear to influence overwinter survival in the present study. Winter duration (defined as the number of degrees where water temperature was less than 10° C) ranged from 160 (1999-2000) to 177 (1998-99) days, which was much longer than the 130 day duration Copeland and Carline (1998) experiment. However, winter duration in this experiment was similar to the 168 day experiment of Jonas and Wahl (1998). This suggests that winter duration was likely not important in the explaining the differential survival rates.

Another potentially important factor in determining the overwinter survival of young fishes is water temperature. Small decreases in water temperature can play a significant role in overwinter survival of YOY fishes, as Johnson and Evans (1991) found that white perch (*Morone chrysops*) raised at 2.5° C suffered significantly higher mortality than those raised at 4° C. The relatively shallow, cement bottom ponds, in combination with the colder air temperatures, likely resulted in water temperatures below 4° C for much of the study. However, yellow perch raised at 2.5° C had lower mortality than yellow perch raised at 4° C (Johnson and Evans 1991). The yellow perch, like the

112

walleye, is considered a coolwater species, and is a much closer relative to walleye than white perch. Thus, these results suggest the low water temperatures realized in this study may have increased YOY walleye survival, not hindered it. It therefore appears that the relatively long winter duration and low water temperature that occurred during this experiment are unable to explain the low YOY walleye survival rates, and that other factors should be considered.

Pre-winter body size and condition may be another factor capable of explaining the overall low survival rates of YOY walleye. The walleye used in this study were smaller than fish used in other YOY walleye overwinter studies (Jonas and Wahl 1998, Copeland and Carline 1998), and they may have been affected by the overwinter period differently than larger fingerlings. However, even some of the smallest pre-winter fish (as small as 4.9 g) survived the winter, suggesting that small pre-winter size did not automatically lead to high overwinter mortality. The walleye were also reared in hatchery conditions and fed an artificial diet until they were transferred to the outdoor rearing ponds, so it is possible that they did not adapt well to the change in conditions. Research on pellet-reared muskellunge has indicated very poor survival, likely due to a combination of poor health, the loss of camouflage markings, and small size (Larscheid et al. 1999). It is possible that similar problems could affect the survival of walleye reared in hatcheries, as they are raised on similar diets and held for similar lengths of time. Length-weight regressions for natural walleye populations typically have a slope > 3 (Carlander 1997), thus the low overwinter survival rate may be explained by the poor body condition of the fish used in this experiment. The pre-winter slope in this study was found to be 2.81, which reduced to 2.67 after winter, suggesting that the fish were in

relatively poor physical condition. Out of the approximately 60 studies reviewed by Carlander 1997, less than 10 populations had slopes < 3, while only two had slopes less than the post-winter slope found in this experiment. Thus, poor body condition may have influenced overwinter survival across years.

Another possible explanation for the low survival rates is that YOY walleye were influenced by density-dependent factors. Overwinter density affected the survival of pumpkinseeds (*Lepomis gibbosus*), as increased densities caused significantly earlier mortality under simulated overwinter conditions (Bernard and Fox 1997). While information about the spatial requirements of overwintering YOY walleye are not known, it is interesting that similar numbers of fish survived each winter (54 in 1997-98, 67 in 1998-99, and 59 in 1999-2000) despite almost a threefold difference in pre-winter density. Thus, it is possible that if initial densities were too high, density-dependent mechanisms may have reduced the populations to similar levels across all years, and led to the observed low survival rate across the three overwinter periods.

In addition to low overall survival, this experiment found mortality to vary greatly among years and among treatments within years, suggesting that other factors may have influenced the survival of YOY walleye in the ponds. Among year variability could potentially be explained by some of the factors discussed above, including among year differences in winter duration, water temperature and rearing density, along with differences in predator effectiveness. Winter duration and water temperature did vary among years, as the number of days with ice cover was 25 % greater in 1997-98 than in 1999-2000, and water temperatures were much lower in October of that year. However, the lowest survival rate arose during the 1999-2000 overwinter period, which had the

shortest period (98 days) of ice cover and similar water temperatures to the winter of 1998-99. Therefore, winter duration and water temperature do not appear to have influenced among year survival variability.

Two factors that seem more capable of explaining the among year survival variation in YOY walleye are rearing density and the species of predator used. Density-dependent overwinter survival has been observed in other temperate species (Bernard and Fox 1997) and the highest yearly survival rate in this experiment coincided with the lowest initial densities, while the lowest survival rate occurred at the highest initial densities. This suggests density-dependent factors may be important in explaining among year variation in survival. In addition, the relationship between yearly survival and the species used as predator seemed to vary among years. Walleye and burbot are both known to actively feed overwinter, but burbot are typically thought to be more of a facilitative piscivore than walleye (Scott and Crossman 1973). In this study, the highest overwinter mortality occurred during the winter when only walleye were used as predators, while the lowest overwinter mortality occurred during the winter when only burbot were used as predators. It is possible that differences in walleye and burbot foraging rates, if both species consumed YOY walleye in a non-size selective manner, could have contributed to the observed yearly variation in overwinter survival.

The observed variation in survival among treatments within years is more difficult to explain. This suggests certain factors were influencing mortality in individual ponds independently, leaving some variation in survival patterns unexplained. Physical and chemical parameters were not extensively monitored within individual ponds, as there was no pre-determined reason to expect significant differences, and periodic sampling of

two most important abiotic variables known to affect fish survival (oxygen and water temperature) indicated that levels found within the ponds were well under the non-lethal limit of YOY walleye. One factor that may explain the within-treatment variation is that other predators were removing fish from the ponds. Mammals, including marten and mink, and piscivorous birds, such as great blue herons and osprey, were observed around the ponds at various times during the study. While the ponds were covered with ice for most of the study period, there was a window of 1 - 2 months when non-piscine predators could access the ponds. Hatchery ponds are popular targets for piscivorous birds, and birds can consume a large proportion of available biomass in a short time period (Glahn et al. 1999). Avian predators would also likely forage in a reverse size-selective manner to that which was expected (e.g. select the largest individuals, Britton and Moser (1982)), and it is possible that the combination of fish and avian predation pressure would explain the absence of size-selective predation obtained in this research as both the largest and smallest individuals would be selectively preyed upon. A final factor that could explain the variation in within treatment mortality is escapement. Holes in the outflow screens or small cracks around the edges of the screens could have been used as escapement routes by the YOY fishes, and any escapement would lead to unexplained survival variation.

Body composition

Only some of the expected physiological relationships were observed in the overwintering YOY walleye. Energy reserves are typically higher in larger fish, as smaller individuals have higher metabolic requirements (Paloheimo and Dickie 1966).

Temperate fishes such as the Colorado squawfish (*Ptychocheilus lucius*) (Thompson et al. 1991), Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) (Berg and Bremset 1998) displayed the expected positive relationship between body size and percent lipid content. The YOY walleye in this study had strong increasing size-specific relationships between body length and absolute lipid and protein mass. However, weak or insignificant size-specific relationships were found between body size and percent dry lipid and protein. Similar results have been previously obtained in pre-winter walleye (Copeland and Carline 1998) and largemouth bass (*Micropterus salmoides*) (Miranda and Hubbard 1994b), but negative relationships between body-size and percent lipid content have been documented for post-winter YOY walleye (Jonas and Wahl 1998, Copeland and Carline 1998) and pumpkinseed (Bernard and Fox 1997). These results suggest the relationship between body-size and specific energy levels in temperate fishes are variable and either species or population specific. A number of surviving walleye had lipid levels below the 2.2 % lipid content suggested as the level required by yellow perch to survive the winter (Newsome and Leduc 1975). This, in combination with the absence of size-dependent overwinter mortality, suggests that the overwinter energetics of walleye and yellow perch are quite different. Walleye are generally much larger than yellow perch going into the overwinter period, which may explain the species-specific relationships.

Overwintering YOY walleye were strongly affected by the presence of a potential predator. Walleye inhabiting predator ponds had significantly higher weight loss (particularly the smaller individuals of the cohort), and had significantly lower post-winter lipid and specific energy levels than their predator-free counterparts. While the long-term physiological effects of co-habitation with predators have not been

117

investigated, short-term stress responses have been observed in a number of fish species (Rehnberg et al. 1987, Järvi 1989, 1990, Huuskonen and Karjalainen 1997). Therefore, one explanation for the observed weight losses and lipid and specific energy differences in the presence of predators could be that the metabolic costs of YOY walleye are increased due to predator-induced stress. Young fishes typically mobilize lipids to support metabolism (Jobling 1995), so the decreased lipid levels in predator exposed fish may support this argument.

An alternate explanation to the effect of predators on YOY walleye energy levels is possible, as Huuskonen and Karjalainen (1997) determined that Eurasian perch (*Perca fluviatilis*), a relative of walleye, actually reduced their metabolic rate when exposed to a potential predator. This was due to their anti-predator response, which was to reduce activity and rely on cryptic colouration to avoid detection. Similar behavioural responses have been observed in young walleye (Wahl 1995, T. Pratt *personal observation*). Therefore, observed weight losses and energy could also be due to the presence of predators restricting the foraging of young walleye, thereby reducing their energy intake and ultimately their growth (Fraser and Gilliam 1992). This could then show up as lower energy reserves and greater reductions in body weight, as was evident in this study.

Changes in activity level could provide a third explanation for the observed differences between predator treatments in YOY walleye overwinter energetic relationships. If walleye display the opposite behavioural response to the cryptic behaviour described above, and become more active in order to avoid predation, one could expect to see the observed reductions in energy reserves. Further study is needed to determine whether the predator-induced reactions observed in YOY walleye were

caused by stress reactions, reduced foraging behaviour, or increases in avoidance behaviour.

Surprisingly, smaller pre-winter fish gained more weight (or lost less weight) than their larger counterparts both in the presence and absence of predation risk. This result was opposite to my prediction that smaller fish would have higher metabolic costs, which would lead to a more rapid decrease in the overall condition of smaller fish as the winter progressed. Similar results were obtained on YOY walleye by Jonas and Wahl (1998), who evaluated the overwinter survival of two fingerling sizes in the presence and absence of prey, and Copeland and Carline (1998), who created groups with different sizes and lipid content by manipulating diets. In the Jonas and Wahl (1998) study, medium-sized fingerlings in both the starvation and fed treatments increased their energy density, while larger fingerlings not fed a diet of minnows lost energy. In addition, Copeland and Carline (1998) found that smaller walleye fingerlings lost less weight than larger fingerlings during their overwinter experiment. These results suggest that either the size-energy relationships determined for smallmouth bass (Oliver et al. 1979, Shuter et al. 1980), pumpkinseed (Bernard and Fox 1997), and yellow perch (Toneys and Coble 1980) are not applicable to walleye, or that the smaller members of a YOY walleye cohort are more able to meet their energy requirements with available winter forage.

One potential explanation for the observed weight and lipid relationships is ontogenetic scaling, which suggests that small individuals may actually be at a competitive advantage over large individuals under specific conditions (Werner 1994, Persson et al. 1998). Growth depends on the ability of an individual to consume a resource and withstand periods of resource depression (Werner 1988). In fishes, size-

119

specific feeding and growth rates decrease with increasing body size (Kamler 1992), and

both foraging and metabolic rates are power functions that vary with body size (Peters

1983; Figure 4.7a). Thus, metabolic costs are fairly consistent across species (Peters

1983, Werner 1988), while foraging gains in fish vary across body sizes primarily due to

attack rate (Persson et al. 1998). Across species, gain curves typically have a lower

power function than metabolic costs (Werner 1994; Figure 4.7a). Thus, under certain

environmental conditions, foraging rates are higher in smaller-sized organisms than the

corresponding metabolic costs, meaning that the net energy available for growth is

greatest at smaller sizes (Werner 1994; Figure 4.7b). Resource availability ultimately

affects foraging rates, and will shift the gain curve in such a way that in times of high

resource availability the optimal size shifts to larger individuals, but in periods of high

competition, smaller individuals hold the competitive advantage (Werner 1994, Persson

et al. 1998).

Overwinter conditions are known to be difficult for temperate YOY fishes (Shuter

and Post 1990), and given the ontogenetic scaling of metabolic and foraging rates, it is

possible that small individuals are capable of out-competing larger individuals. While not

much attention has been given to the concepts of ontogenetic scaling in fishes, Persson et

al. (1998) have developed the theory to explain the influence of competitive interactions

on roach (*Rutilus rutilus*) and vendace (*Coregonus albula*) population cycles. The size-

dependent differences in weight and specific energy found in this research appear to

support the theory of ontogenetic scaling, as smaller fishes appeared to out-compete

larger individuals despite their higher metabolic costs. Given that many of the fish used

in this experiment gained weight, it is apparent that they were feeding during the
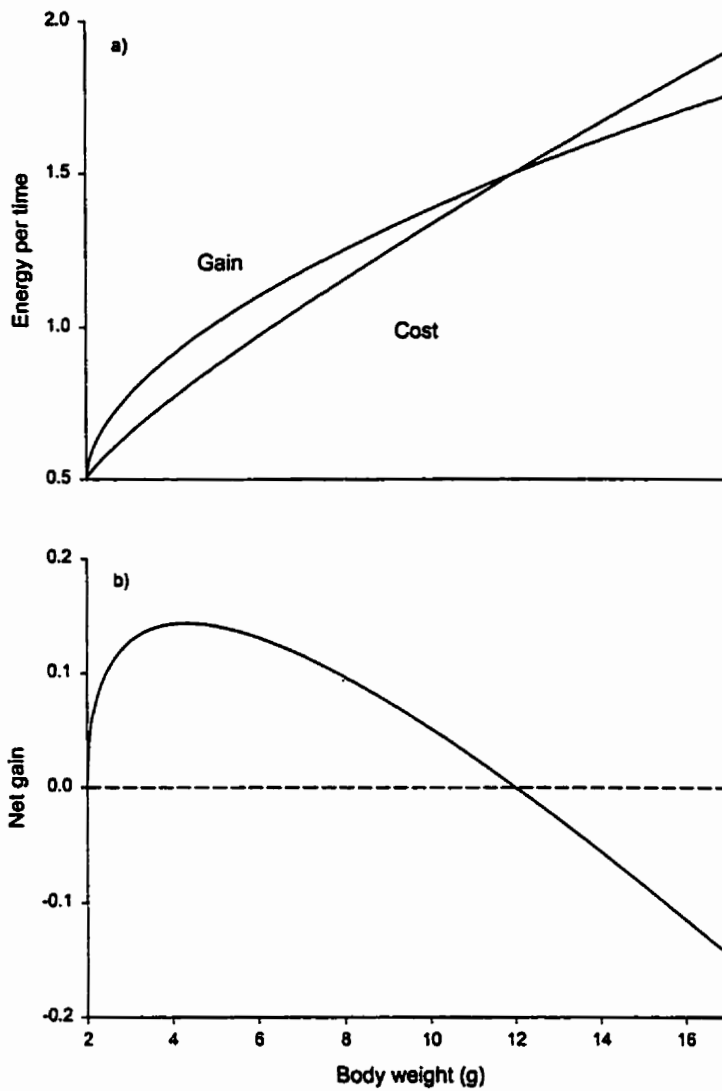
Figure 4.7. a) Theoretical cost and gain curves as a function of body weight, and b) the

net gain curve as a function of body weight. The dashed line in b) represents zero net

gain. Figure was modified from Werner (1994).

121

overwinter period, and that ontogenetic scaling may explain the size-dependent relationships observed here.

An alternate explanation to the observed weight change patterns is that smaller YOY walleye increased their mass by taking on water. Smaller walleye, particularly those in the predator-free and pre-winter treatments, contained significantly higher percentages of water than larger walleye. However, the fact that percent lipid levels in walleye reared in predator-free ponds were higher than those in pre-winter fish suggests that these individuals were feeding overwinter. Thus, the weight change patterns may partially be explained by fluctuating water content, but some of the observed pattern may also be explained by ontogenetic scaling.

The results from this research suggest that, although the first overwinter period can be a time of significant mortality in walleye populations, mortality did not occur in a size-dependent manner. While the first winter may be an important period in understanding recruitment variability in walleye, size-specific predation and size-dependent physiological processes were unable to explain the observed survival patterns. This study is the third in recent years to find no evidence for size-dependent overwinter mortality in YOY walleye under controlled conditions, and the first to include potential predators as part of the study design. Size-selective predation has led to size-dependent overwinter mortality in yellow perch (Post and Evans 1989a), and possibly in native walleye populations (Chevalier 1973, Forney 1976). However, given the relatively large pre-winter size obtained by most YOY walleye populations and the absence of size-specific energetic costs, it is probable that size-dependent overwinter mortality would be rarely observed in many walleye populations.

Appendix 4.1. Raw data used to determine the change in overwinter body weight (wet

weight) by treatment from the three overwinter periods.

1997-98			1998-99			1999-2000		
Pre-weight (g)	Post-weight (g)	Treatment	Pre-weight (g)	Post-weight (g)	Treatment	Pre-weight (g)	Post-weight (g)	Treatment
7.6	7.24	Pred	7.7	7.3	Pred	5.6	5.66	Pred
9.3	8.71	Pred	7.4	5.97	Pred	5.6	5.94	Pred
9.8	9.24	Pred	7.7	7.18	Pred	6.2	5.4	Pred
11.4	9.82	Pred	8	7.29	Pred	7.3	8.19	Pred
13.2	12.79	Pred	8.3	8.25	Pred	8.1	11.42	Pred
13.9	13.64	Pred	8.5	7.93	Pred	8.4	9.43	Pred
15.2	14.23	Pred	8.7	9.35	Pred	9	8.69	Pred
5.7	5.51	Pred	6.3	8.33	Pred	9.4	8.03	Pred
5.7	5.15	Pred	9	8.51	Pred	9.7	7.82	Pred
7.2	7.24	Pred	9.7	8.61	Pred	10.8	7.27	Pred
7.6	7.02	Pred	9.8	9.32	Pred	5.6	10.61	Pred
8	7.94	Pred	10.1	9.18	Pred	5.6	5.77	Pred
8.7	8.4	Pred	10.3	9.43	Pred	5.8	28.55	Pred
9.4	8.46	Pred	11	10.64	Pred	6.5	8.13	Pred
9.4	8.6	Pred	11.8	9.98	Pred	6.6	5.92	Pred
9.6	9.06	Pred	12.1	10.65	Pred	6.9	6.22	Pred
9.7	8.9	Pred	12.6	11.35	Pred	8.3	5.59	Pred
9.8	9.36	Pred	13.3	11.37	Pred	8.3	10.6	Pred
10	9.69	Pred	7.7	12.33	Pred	8.4	7.94	Pred
10.1	9.38	Pred	7.4	12.97	Pred	9.4	7.13	Pred
10.3	9.68	Pred	6.7	7.3	Nopred	4.9	7.25	Pred
10.5	9.88	Pred	6.8	7.22	Nopred	4.9	6.78	Pred
10.5	10.11	Pred	6.8	7.04	Nopred	5.3	9.27	Pred
10.7	10.07	Pred	8.3	8.41	Nopred	5.5	9.42	Pred
10.8	10.39	Pred	8.5	8.6	Nopred	5.6	13.22	Pred
11.5	10.87	Pred	8.5	8.74	Nopred	5.8	8.52	Pred
11.8	11.25	Pred	8.6	8.85	Nopred	5.9	6.26	Nopred
12.3	11.38	Pred	8.7	8.17	Nopred	5.9	5.32	Nopred
12.8	11.68	Pred	8.8	8.89	Nopred	6.4	8.18	Nopred
13.5	13.52	Pred	8.8	8.71	Nopred	6.5	7.42	Nopred
13.5	12.84	Pred	9.5	9.81	Nopred	6.7	10.56	Nopred
14	13.76	Pred	9.7	9.45	Nopred	6.7	8.22	Nopred
14.7	13.73	Pred	10.2	9.84	Nopred	7.1	7.77	Nopred
14.8	13.62	Pred	10.3	10.81	Nopred	7.2	7.91	Nopred
15.6	15.96	Pred	10.3	11.11	Nopred	7.2	6.95	Nopred
16.8	15.6	Pred	10.5	9.94	Nopred	7.4	6.09	Nopred
17	16.89	Pred	10.9	10.38	Nopred	7.5	9.3	Nopred
17.1	16.62	Pred	11.1	10.83	Nopred	7.5	8.02	Nopred
18.4	16.78	Pred	11.2	11.01	Nopred	7.6	5.97	Nopred
94	5.6	Nopred	11.2	10.96	Nopred	8.5	7.37	Nopred
93	7.4	Nopred	11.5	12.2	Nopred	9.2	6.97	Nopred
102	8.1	Nopred	11.6	11.26	Nopred	9.7	5.45	Nopred
114	12.1	Nopred	12	11.47	Nopred	10.3	7.56	Nopred
118	12.2	Nopred	12.2	11.87	Nopred	10.8	13.92	Nopred

123

114	12.6	Nopred	12.4	11.59	Nopred	14.7	9.99	Nopred
122	13.9	Nopred	6.6	6.66	Nopred	5.4	8.73	Nopred
128	14.7	Nopred	6.8	6.97	Nopred	5.7	6.1	Nopred
130	16.3	Nopred	7.4	7.88	Nopred	5.8	11.27	Nopred
128	16.5	Nopred	7.7	7.84	Nopred	6.9	5.82	Nopred
134	19	Nopred	8	8.09	Nopred	7.6	7.73	Nopred
97	6.4	Nopred	8.2	7.65	Nopred	10	5.65	Nopred
99	9.8	Nopred	8.2	8.51	Nopred	10.6	7.02	Nopred
115	10.9	Nopred	8.3	8.57	Nopred	4.9	7.85	Nopred
115	11.6	Nopred	9	8.5	Nopred	4.9	5.86	Nopred
			9.4	9.69	Nopred	5.3	6.22	Nopred
			9.4	9.33	Nopred	5.5	12.43	Nopred
			10	9.66	Nopred	5.6	7.91	Nopred
			10.4	9.78	Nopred	5.8	6.66	Nopred
			10.4	10.21	Nopred	5.9	11.4	Nopred
			10.7	10.36	Nopred			
			10.8	9.43	Nopred			
			11	10.64	Nopred			
			12.1	12.16	Nopred			
			12.7	12.75	Nopred			
			13	12.5	Nopred			
			13.9	13.77	Nopred			
			122	15.22	Nopred			

Appendix 4.2. Raw data by treatment for body composition variables taken from walleye used in the 1999-2000 study.

Pond	Trt	prewt (g)	wetwt(g)	drywt (g)	lipwt (g)	ptnwt (g)	% lipid	% ptn	% water	energy
1	Pred	98	6.99	1.48	0.10	1.14	10.299	83.846	78.89	3.461439
1	Pred	94	5.50	1.22	0.29	0.75	32.048	70.238	77.848	3.383454
1	Pred	93	5.79	1.20	0.13	0.87	15.604	79.593	79.295	3.283239
1	Pred	116	8.08	1.72	0.22	1.22	20.012	79.821	78.741	3.645533
1	Pred	104	7.53	1.63	0.21	1.16	20.036	79.857	78.406	3.599666
1	Pred	89	4.91	1.05	0.12	0.75	15.375	77.874	78.506	3.147096
1	Pred	106	8.12	1.81	0.18	1.33	15.883	81.903	77.781	3.670349
1	Pred	106	7.82	1.74	0.25	1.22	21.78	79.223	77.761	3.667012
1	Pred	105	8.98	2.06	0.26	1.48	20.917	81.222	77.098	3.827728
1	Pred	110	10.95	2.35	0.28	1.66	20.65	80.963	78.567	3.932563
2	Pred	106	8.18	1.77	0.20	1.29	18.127	81.376	78.326	3.671998
2	Pred	111	10.14	2.26	0.56	1.36	37.868	72.672	77.708	3.988547
2	Pred	102	7.75	1.70	0.32	1.12	27.874	75.707	78.061	3.673248
2	Pred	91	5.56	1.17	0.16	0.82	19.641	77.468	78.983	3.282609
2	Pred	99	6.72	1.41	0.19	1.01	19.62	79.158	78.959	3.466286
2	Pred	118	12.51	2.83	0.30	2.05	19.301	83.076	77.359	4.109575
2	Pred	107	8.78	1.96	0.36	1.30	28.138	76.745	77.647	3.80843
2	Pred	94	6.01	1.20	0.09	0.90	10.426	81.267	79.958	3.247129
2	Pred	88	5.28	1.10	0.13	0.79	16.92	78.527	79.117	3.211795
2	Pred	111	10.21	2.16	0.21	1.60	16.25	83.206	78.88	3.847147
2	Pred	102	7.84	1.78	0.26	1.26	22.235	79.819	77.272	3.701223
2	Pred	96	6.90	1.52	0.18	1.13	17.591	81.722	78.035	3.536684
2	Pred	96	6.44	1.35	0.12	1.01	13.743	81.864	79.099	3.391241
2	Pred	106	8.90	1.97	0.32	1.37	25.303	79.248	77.886	3.811752
2	Pred	143	11.72	2.41	0.26	1.74	19.122	82.016	79.39	3.955871
3	Nopred	90	5.62	1.27	0.21	0.89	22.851	77.947	77.454	3.396198
3	Nopred	100	8.03	1.73	0.31	1.18	27.117	77.467	78.471	3.701697
3	Nopred	83	4.99	1.08	0.17	0.75	21.445	76.585	78.378	3.225478
3	Nopred	102	7.20	1.72	0.33	1.15	28.604	76.609	76.164	3.701075
3	Nopred	98	7.66	1.50	0.24	1.04	23.873	77.906	80.474	3.547385
3	Nopred	97	7.70	1.78	0.41	1.14	33.887	74.644	76.899	3.769482
3	Nopred	100	7.36	1.64	0.26	1.14	23.6	78.526	77.705	3.630858
3	Nopred	96	6.58	1.52	0.27	1.04	25.95	77.101	76.897	3.5758
3	Nopred	97	6.95	1.60	0.29	1.09	26.709	77.258	77.051	3.627004
3	Nopred	86	5.02	1.13	0.16	0.82	19.606	79.026	77.406	3.276012
3	Nopred	98	7.41	1.76	0.38	1.09	31.43	72.618	76.302	3.704713
3	Nopred	120	13.39	2.90	0.23	2.14	15.272	83.931	78.316	4.104242
3	Nopred	96	6.49	1.40	0.14	1.05	14.735	81.923	78.377	3.439892
3	Nopred	109	10.13	2.33	0.38	1.62	26.488	79.893	76.971	3.976266
3	Nopred	108	9.64	2.22	0.44	1.46	31.429	77.067	77.023	3.951267
3	Nopred	90	5.68	1.27	0.32	0.77	34.304	69.722	77.686	3.438198
3	Nopred	92	5.59	1.15	0.16	0.81	19.181	77.356	79.391	3.263008
3	Nopred	103	8.21	1.82	0.27	1.32	22.812	81.191	77.864	3.743263
3	Nopred	112	10.72	2.53	0.43	1.74	28.572	79.921	76.412	4.066302
3	Nopred	105	8.76	2.11	0.51	1.33	36.093	74.473	75.868	3.935357

125

3	Nopred	97	6.74	1.47	0.17	1.09	17.433	81.218	78.143	3.503441
3	Nopred	87	5.89	1.29	0.24	0.87	26.069	75.671	78.183	3.417989
3	Nopred	98	7.46	1.78	0.46	1.08	36.868	71.862	76.171	3.771749
3	Nopred	93	9.64	1.27	0.15	0.93	16.999	80.66	86.872	3.360348
3	Nopred	88	5.16	1.16	0.28	0.72	32.126	70.367	77.57	3.343752
3	Nopred	96	7.28	1.67	0.39	1.05	33.38	73.166	77.038	3.694623
3	Nopred	82	4.23	0.90	0.13	0.62	19.078	75.036	78.844	3.017552
4	Nopred	110	11.38	2.81	0.56	1.89	33.047	79.36	75.288	4.196474
4	Nopred	92	6.02	1.44	0.28	0.97	27.88	75.878	76.05	3.538324
4	Nopred	89	5.95	1.38	0.29	0.92	29.06	75.434	76.773	3.511784
4	Nopred	97	6.62	1.47	0.21	1.04	20.877	78.931	77.819	3.510458
4	Nopred	90	5.48	1.26	0.24	0.85	26.481	75.206	76.989	3.401731
4	Nopred	108	10.23	2.47	0.43	1.69	28.881	79.661	75.91	4.045434
4	Nopred	102	7.17	1.78	0.40	1.16	32.651	75.357	75.244	3.761842
	Pre	108	9.86	2.22	0.31	1.59	23.185	81.484	77.494	3.92038
	Pre	94	6.04	1.38	0.25	0.95	25.324	76.616	77.074	3.483453
	Pre	100	7.60	1.60	0.26	1.13	23.806	79.181	78.899	3.622237
	Pre	102	8.13	1.71	0.19	1.28	17.381	82.692	78.966	3.65178
	Pre	100	7.66	1.58	0.23	1.32	22.161	88.881	79.367	3.717389
	Pre	91	5.26	1.12	0.43	0.56	47.688	58.812	78.678	3.397243
	Pre	113	11.21	2.69	0.56	1.77	34.315	77.949	76.013	4.154354
	Pre	104	8.61	1.96	0.38	1.15	29.365	70.272	77.188	3.738279
	Pre	101	7.86	1.63	0.16	1.24	15.118	83.297	79.255	3.593711
	Pre	100	7.63	1.64	0.22	1.20	20.163	80.95	78.485	3.623936
	Pre	107	9.64	2.04	0.21	1.52	17.353	83.227	78.831	3.811831
	Pre	92	5.51	1.17	0.29	0.73	32.34	70.736	78.724	3.361306
	Pre	95	6.16	1.30	0.13	0.98	15.075	81.787	78.862	3.376836
	Pre	101	7.89	1.67	0.17	1.27	15.719	83.506	78.808	3.625087
	Pre	88	4.28	0.83	0.20	0.51	29.77	68.388	80.682	3.011842
	Pre	95	6.26	1.36	0.25	0.93	26.177	76.471	78.332	3.473828
	Pre	98	7.06	1.61	0.35	1.04	31.563	74.506	77.211	3.656842
	Pre	88	4.36	0.89	0.01	0.71	1.896	84.739	79.689	2.918786

Chapter 5.

The Relative Contribution and Survival of Two Stocked Walleye Fingerling Sizes in Six Eastern Ontario Lakes

5.1. Introduction

Understanding the role of body size in stocking success is an important consideration for fishery managers. The early life history of fishes is a period of high and variable mortality, and recruitment patterns are typically set during this time (Houde 1987, 1989). Increasing size typically reduces mortality in juvenile fishes (Peterson and Wroblewski 1984, Houde 1987), and as such, increasingly larger fish are being used as the stocking size of choice. The effect of body size on the survival of stocked individuals has been studied in a number of species, including arctic grayling (*Thymallus thymallus*), channel catfish (*Ictalurus punctatus*), muskellunge (*Esox masquinongy*), striped bass hybrids (*Morone saxatilis * M. chrysops*) and walleye (*Stizostedion vitreum*) (Jennings and Phillip 1992, Santucci et al. 1994, Carlstein 1997, Larscheid et al. 1999, McKeown et al. 1999, Wesley et al. 1999).

Walleye are one of the most heavily stocked and highly prized sport fish in North America. In an effort to create or maintain healthy recreational and commercial fisheries, walleye have been stocked in North American waters for over 100 years (Laarman 1978, Ellison and Franzin 1992). The widespread availability of successful fish culture techniques means a number of walleye life stages can be stocked at different times during the fish's life cycle, including eyed eggs, sac-fry, a variety of fingerling sizes, juveniles, or even adults (Kerr and Seip 1994, Larscheid 1995). Currently, fingerlings are the most

127

commonly stocked life stage, though differences in rearing practices mean that walleye produced as fingerlings can vary greatly in size, age, and body condition between hatcheries.

The cost of producing an individual fish for each of the aforementioned life stages increases with the length of time required to rear the fish in a hatchery. However, the presumed benefit of growing walleye to a larger size before stocking is an increase in the survival rate of individual fish (Santucci and Wahl 1993). As hatchery resources are limited, the production costs of a particular life stage must be balanced against the likelihood of survival in a given waterbody. Unfortunately, walleye recruitment is variable and remains poorly understood (Madenjian et al. 1996, Johnson et al. 1996) and the success of stocking a particular walleye life stage is quite variable even within lakes (Schneider 1983, Jennings and Philipp 1992). Therefore, it should not be surprising that the outcome of walleye stocking events remain largely unpredictable.

Many studies have been performed to determine whether walleye stocking has led to the recruitment of stocked individuals into the population (reviews by Laarman 1978, Ellison and Franzin 1992), and much work has been focused on determining whether increasing size-at-stocking results in higher survival rates (e.g. Jennings and Philipp 1992, Koppelman et al. 1992, Paragamian and Kingery 1992, Mitzner 1992, McWilliams and Larscheid 1992). Unfortunately the results from these studies have not shown a single stocking stage capable of forming a strong year class across waterbodies, which has led, in many cases, to management agencies analyzing stocking events on a lake-by-lake basis. If any generalities can be taken from the above research, fry are thought to be the most cost effective life stage in lakes where walleye are being introduced for the first

time and centrarchid densities are low (Forney 1975, Kraai et al. 1985). Due to high cannibalism, intra- and inter-specific competition, and predation risk, in lakes with strong walleye populations (Forney 1976) and in communities dominated by centrarchids (Santucci and Wahl 1993), advanced fingerlings are thought to be the most effective stocking size.

Despite the numerous studies performed to determine which size-at-stocking is most effective, multi-lake studies are rare, very few small lakes have been investigated (but see Jennings and Philipp 1992), and no research has been done in Canadian lakes. Current Ontario Ministry of Natural Resources hatchery practices involve rearing walleye in outdoor rearing ponds until late June, when they can be stocked as summer fingerlings, or moved indoors and reared intensively on a pellet diet until early fall when they are stocked as fall fingerlings.

The first objective of this study was to determine whether size differences existed between summer and fall fingerlings at the time when fall fingerlings were stocked. The second objective was to determine the relative contribution and relative survival rate of stocked summer and fall walleye fingerlings to the adult population in six small eastern Ontario lakes, while the final objective of this research was to investigate the relative contribution of hatchery fish to the walleye population as a whole. Based on the hypotheses that mortality decreases with increasing body size, and that body size prior to winter differs between the fingerling types, I predicted that summer fingerlings would survive better than fall fingerlings, and contribute more individuals to the fishery.

5.2. Methods

Study areas

Four eastern Ontario lakes (Big Clear, Flower Round, Sand (Bedford), and

Thirteen Island) were stocked by the Ontario Ministry of Natural Resources (OMNR)

with summer and fall fingerlings in 1992 and 1993 for the purpose of a paired-plant

assessment during the course of an intensive ten-year walleye stocking study (see Seip

1995). Flower Round Lake was also given paired-plants in 1990 and 1991. As part of

the current study, two additional eastern Ontario lakes (Black and Warrens) were planted

with summer and fall fingerlings in 1998 (Figure 5.1). All six lakes are relatively small,

ranging in size from 25 - 337 hectares, and have similar physical characteristics (Table

5.1). The potential productivity of the lakes varies widely, ranging from unproductive

(Sand (Bedford) to highly productive (Big Clear and Warrens) on the basis of their

morphoedaphic indices (Ryder et al. 1974).

Fish communities in the lakes

Fish community composition varied widely across lakes. Only three species,

northern pike (*Esox lucius*), pumpkinseed (*Lepomis gibbosus*), and walleye were

common to all six lakes (Table 5.2). Big Clear, Black, and Thirteen Island lakes had the

most complex communities, with eleven species occurring in each, while Warrens Lake

had the simplest fish community with only six species. Big Clear Lake was the only

waterbody where walleye were considered abundant; the other five populations all had

130
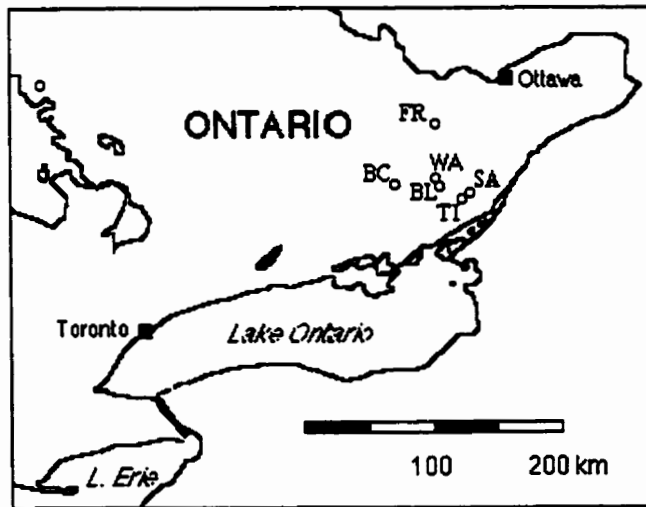
Figure 5.1. Location of the six eastern Ontario study lakes. Lake abbreviations: BC=Big

Clear, BL=Black, FR=Flower Round, SA=Sand (Bedford), TI=Thirteen Island, WA=

Warrens.

131

Table 5.1. Physical characteristics and the potential productivity of the six waterbodies

selected for the walleye paired-plant assessment. The potential lake productivity was

estimated using the morphoedaphic index (MEI), which uses the total dissolved solids

(TDS) and the mean depth to determine a rough measure of each lakes' productive

capacity.

Lake	Lake characteristics							
	Lat.	Long.	Surface area (ha)	Perim. (km)	Mean depth (m)	Max. depth (m)	TDS (mg/L)	MEI
Big Clear	44°43'	76°55'	337.0	14.5	6.6	18.3	145	22.0
Black	44°47'	76°46'	39	3.2	7.8	22.3	116	14.9
Flower Round	45°10'	76°41'	97.2	5.3	6	12.8	94	15.7
Sand (Bedford)	44°34'	76°35'	24.8	2.9	8.2	25.9	44	5.4
Thirteen Island	44°32'	76°38'	105.7	13.8	6.9	25.9	85	13.3
Warrens	44°49'	76°44'	36	2.5	2.6	7.3	87	33.5

Table 5.2. A summary of the fish communities captured by trapnet from six eastern Ontario lakes. Data displayed indicate a measure of relative abundance (measured as catch-per-unit effort).

Species	Lake CUE					
	[a]Big Clear	[a]Flower Round	[a]Sand (Bedford)	[a]Thirteen Island	[b]Black	[b]Warrens
burbot *Lota lota*	0.1	-	-	-	-	-
northern pike *Esox lucius*	1	0.8	0.1	3.2	0.4	1.5
white sucker *Catostomus commersoni*	1.2	4.0	-	2.6	0.3	2.0
brown bullhead *Ameiurus nebulosus*	8.5	14.0	-	0.4	0.1	18.6
rock bass *Ambloplites rupestris*	6.4	9.9	7.1	2.5	5.3	-
largemouth bass *Micropterus salmoides*	7.5	2.9	0.3	1.0	0.2	-
smallmouth bass *Micropterus dolomieui*	2.3	1.8	0.5	1.3	2.0	-
pumpkinseed *Lepomis gibbosus*	34.6	1.8	0.3	22.4	6.1	4.2
bluegill *Lepomis macrochirus*	52.2	-	-	9.0	8.0	-
black crappie *Pomoxis nigromaculatus*	-	-	-	24.0	7.0	-
yellow perch *Perca flavescens*	0.7	-	31.4	2.9	0.7	13.8
walleye *Stizostedion vitreum*	8.4	2.0	2.8	0.1	0.2	1.0
Total centrarchid	103	16.4	8.2	60.2	28.6	4.2

[a] Data from pre-study standard OMNR index trapnetting (Seip 1995)

[b] Trapnetting data from this study

marginal walleye populations. Centrarchid densities were highest in Big Clear and Thirteen Island lakes, moderate in Black Lake, and relatively low in Flower Round, Sand (Bedford) and Warrens lakes.

Strain and stocking

All stocked walleye originated from the OMNR's White Lake Fish Culture Station. Eggs and sperm were obtained in the spring from Napanee River (a Lake Ontario tributary) parental stock. Eggs were reared in incubation jars in the hatchery, and one or two day old fry were transferred to fertilized outdoor rearing ponds. The young walleye remained in these ponds for approximately 2 months, at which time the ponds were drained and the walleye removed. Summer fingerlings (SF) were either stocked at this time in the study lakes, or transferred indoors into circular rearing tanks. The latter were initially reared on a diet of Biokiowa™, then switched to a standard OMNR trout pellet diet. These fish were marked with a pelvic fin clip in August, and stocked in September as fall fingerlings (FF). Complete rearing, marking, and stocking procedures are in available in Seip (1995). Despite attempts to standardize rearing procedures, there was some variation in the weights of the fish stocked in different lakes and years (Table 5.3).

Young-of-year (YOY) walleye from the 1992 and 1993 plantings were stocked at the standard OMNR densities (summer fingerlings 125/ha, fall fingerlings 25/ha) with the assumption that mortality of summer fingerlings would reduce their numbers to roughly that of fall fingerlings by the time the fall fingerlings were stocked. As stocking a complete complement of summer and fall fingerlings is essentially doubling the

134

Table 5.3. Mean weight, date of stocking, and total number stocked by lake for the summer (SF) and fall (FF) fingerlings assessed in this study.

Year	Lake	Summer fingerlings			Fall fingerlings		
		Weight (g)	Date	Total # stocked	Weight (g)	Date	Total # stocked
1990	Flower Round	0.65	July 6	12000	11.3	Sept 7	2450
1991	Flower Round	0.39	July 3	12000	14.3	Sept 4	2450
1992	Big Clear	0.53	July 4	42000	8.8	Sept 9	8420
	Flower Round	0.74	June 30	12000	11.9	Sept 1	2450
	Sand (Bedford)	0.55	July 3	3100	11.0	Sept 2	650
	Thirteen Island	0.55	July 3	13200	11.0	Sept 2	2774
1993	Big Clear	0.97	July 3	42000	9.3	Sept 8	8420
	Flower Round	0.97	July 3	12000	8.9	Sept 7	2450
	Sand (Bedford)	0.64	July 4	3100	7.1	Aug 30	650
	Thirteen Island	0.64	July 7	13200	9.5	Sept 9	2774
1998	Black	0.91	June 24	2525	10.4	Sept 9	500
	Warrens	0.91	June 24	2150	10.4	Sept 9	420

135

estimated sustainable walleye biomass in each lake, the 1998 plantings were stocked at one-half the density of the 1992-93 plantings. Stocked walleye have been found to introduce significant intraspecific competition effects (Li et al. 1996a; 1996b), thus it was hoped that stocking at one-half densities would reduce the potential for competition between the two stocking stages to affect the outcome of the study.

The actual stocking procedure was identical for both summer and fall fingerlings. Walleye were loaded onto a hatchery truck, and driven to each lake. The furthest driving distance was approximately 70 km. Stocking was conducted during the daylight hours, and all fish were stocked from shore in the same general area in each lake over rocky substrate.

Stocking evaluation

(i) 1992-93 plantings

YOY and yearling walleye were collected from the 1992 and 1993 plantings in Big Clear and Sand (Bedford) lakes by electrofishing with a Smith-Root Type VI-A model, mounted on a 5.2 m boat with a Kohler XL series generator (Table 5.4). The voltage and pulse width were varied to suit the conductivity of the waters and to maintain a current optimal for capturing YOY walleye (approximately 5.0 A). The electrofishing of Sand (Bedford) Lake took place during the summer of 1993, whereas Big Clear Lake was electrofished in the fall of 1993. YOY and yearling walleye were also collected from Flower Round Lake using smallmesh gillnets. Sixteen (eight 25.4 mm and eight 38.1 mm bar measure) 7.6 m monofilament nylon gillnet panels were set overnight perpendicular to shore in Flower Round Lake during the fall of 1992.

136

Table 5.4. List of sampling technique and target life stage by year in each of the six study lakes.

Lake	Year	Assessment	Target life stage
	1993	fall electrofishing	YOY
Big Clear	1997	winter angler head collection	adult
		summer trapnet	adult
	1998	summer angler head collection	adult
	1998	fall gillnet	YOY
Black	1999	fall trapnet	yearling
Flower Round	1991	fall gillnet	YOY
	1992	fall gillnet	YOY, yearling
	1997	summer trapnet	adult
		fall gillnet	adult
	1998	fall gillnet	adult
	1999	fall gillnet	adult
Sand (Bedford)	1992	fall electrofishing	YOY
	1993	fall electrofishing	YOY, yearling
	1997	summer trapnet	adult
		summer angler head collection	adult
Thirteen Island	1997	summer trapnet	adult
		summer angler head collection	adult
Warrens	1998	fall gillnet	YOY
	1999	fall trapnet	yearling

No further collections were made on these four lakes until 1997, when an intensive trapnetting, gillnetting, and angler otolith collection campaign was initiated. As the target of these collections was as large a sample size as possible from each lake, no standardized sampling protocol was employed. Initially, anglers were asked to collect walleye heads with pelvic fins attached during the 1997 ice fishing season. Anglers were also asked for the length and weight of each fish submitted. Only one waterbody, Big Clear Lake, provided an abundant contribution of walleye heads through this voluntary collection method. Big Clear Lake anglers contributed > 200 heads, while the only other submissions were three heads from Sand (Bedford) and one head from Thirteen Island lakes anglers. All contributed walleye were checked for a pelvic fin clip, and the otoliths were extracted. As fall fingerlings had all been marked with a pelvic fin clip, they could be readily identified upon visual inspection, but otolith interpretation was required to determine the origin (either SF or native) of non-clipped fish (Casselman 1994).

Big Clear, Flower Round, Sand (Bedford), and Thirteen Island lakes were also trapnetted from June-October 1997. Four identical 6 ft (2.1 m) trapnets were set for 24 hr, and checked for walleye each morning. Each net had a 7 ft (2.4 m) box, with 1.5" (stretched) mesh. Trapnetting effort was similar on three of the lakes, but was lower on Big Clear Lake due to a large sample provided from the angling community on that particular waterbody. Total effort ranged from 48 trapnet lifts in Thirteen Island Lake, 44 lifts in both Flower Round and Sand (Bedford) Lakes, and 16 lifts in Big Clear Lake. All walleye of a predetermined size range (estimated from walleye growth rates determined by previous OMNR research on these waterbodies) were kept from the trapnet collections, and were euthanized by CO_2 asphyxiation in an ice water slurry. The

collected fish were then weighed and measured (fork length), the pelvic fins were inspected for evidence of a fin clip, and the fish were then frozen for later removal of the otoliths.

Due to continued low sample sizes, a fall gillnetting program was established in Flower Round Lake in 1997, which continued through 1998-99. A variety of stretched mesh sizes (2", 2.5", 3", and 4") were set in 200 ft gangs for 24 hr perpendicular to shore. The nets were fished for a total of 18 days over the three year period. Walleye captured were measured (FL), checked for a pelvic clip, and returned to the lab for otolith extraction.

(ii) 1998 Plantings

YOY walleye were collected from Black and Warrens lakes in the fall of 1998 and spring of 1999 using 1" and 1.5" (stretched mesh) gillnets. Nets were tied in 200 ft gangs, fished for 24 hr periods, and checked daily. Nets were fished for a total of eight days in Warrens Lake, and sixteen days in Black Lake. Captured walleye were measured (FL), checked for a pelvic clip, and returned to the lab for otolith extraction.

A collection was made in Black and Warrens Lakes in the fall of 1999 using 6 ft trapnets. Warrens Lake was netted for three overnight sessions, and yearling walleye were measured (FL) and released, as otolith interpretation from fish collected earlier indicated no natural reproduction. Black Lake was netted for 8 evenings, but no yearling walleye were captured.

Otolith examination

To classify origin, one of the two sagittal otoliths extracted from each walleye were prepared for microstructure examination by grinding and polishing the lateral side. The otolith was then epoxied to a microscope slide, and after hardening, the medial side was ground and polished. To grind and polish the otolith, moderately coarse to progressively finer grit disks and aluminum oxide lapping film were used (Casselman 1994). Following quantifiable criteria developed by Casselman (1994), otolith microstructure were examined at 100 and 150x magnification for characteristics associated with stocked walleye. Results from this technique are not definitive, and known error rates typically range from 5 – 10 % (Casselman 1994). The known error rate from this study, as calculated by comparing the origin and age of clipped walleye with the stocking records for each lake, was somewhat higher (17%), possibly due to the inaccurate dating of heads submitted by anglers.

Walleye were aged in order to determine whether they had been stocked during either the 1992-93 or 1998 time period. This was necessary, as plantings had occurred prior to 1992 on all the study lakes. The otoliths were also used to determine the age and back-calculated length-at-age of each fish. The second sagittal otolith was sectioned inversely, ground, polished, and digitized using Calcified Structure Age Growth data Extraction Software (CSAGES) software (Casselman 1994). All age interpretations were digitized at 61.7x magnification using a radial line that intersected the origin and extended along the sulcus in the ventral direction. Age and growth trajectories were then

taken from the output provided by the CSAGES program, and determined from the formula below.

Data analysis

Evidence for size differences in YOY and yearling walleye between fish planted as summer and fall fingerlings were investigated a number of ways. Initially, the length and weight at age-0 and age-1 for individuals from the 1992-93 year-classes were compared, along with fish identified as native in origin, using one-way analyses of variance (ANOVA). Assessments of length-at-age differences between summer and fall fingerlings and fish of native origin that survived to the adult stage were also undertaken with one-way ANOVA's. Where possible, analyses were done on individual lakes, but due to low sample sizes, a final analysis was also performed using pooled length-at-age data from lakes where growth rates did not differ significantly. Length-at-age was determined using the Fraser-Lee method (Busacker et al. 1990), where:

$$L_x = [(TL - i) * (S_x / SL)] + i$$

and L_x = length-at-age x, S_x = scale length at age x, SL = scale length, TL = total length, and i = scale length vs body length intercept. A value of 55 was assumed for the intercept (Carlander 1982), as sample sizes were low in most cases. Growth differences between summer and fall fingerlings were also investigated by comparing lengths of yearling walleye from the 1998 planting in Warrens Lake using a Student's t-test. A final size comparison was performed by comparing the weight of YOY walleye collected in mid-October (either summer fingerling or native fish) with the weight of hatchery walleye used in the size-dependent overwinter mortality experiment (Chapter 4) across

141

years. No statistics were performed on these data as any comparison would likely underestimate the true size of fall fingerlings stocked in September, and their growth potential in the wild is likely higher than it is in the hatchery. Nevertheless, the relationship was included as it illustrates the potential for growth differences in the two fingerling sizes.

The relative contribution of summer and fall walleye fingerlings to the fishery was determined by comparing the number of each planting recovered with its associated binomial probability. It was assumed that the probability of capturing a summer or fall fingerling was equal (i.e. $P = 0.5$), and therefore the probability of capturing a specific number of individuals could be determined by calculating the binomial probability (Zar 1999). The probability of capturing summer and fall fingerlings was determined for each sampling period in order to determine whether trends changed over time within a lake.

In order to compare relative survival rates, the number of summer fingerlings captured were divided by 5 (as summer fingerlings were stocked at 5 times the density of fall fingerlings). A Student's t-test was performed to determine whether the survival ratio differed from 1 : 1 for adult walleye from the 1992-93 year-classes across Big Clear, Sand (Bedford), and Thirteen Island lakes. Flower Round was not analyzed, as no fall fingerlings were captured from that lake.

The paired-plant experiment was initiated at the end of a ten-year walleye stocking project (Seip 1995). Thus, the origin of individual fish determined by this study allows the contribution of hatchery individuals to the population as a whole to be investigated. To determine the overall contribution of hatchery individuals, fish

identified as arising from the 1984-92 year-classes from Big Clear, Flower Round, Sand (Bedford), and Thirteen Island lakes were examined for either a native or hatchery origin.

5.3. Results

Growth differences between summer and fall fingerlings

In general, size differences were observed in the direction predicted between the length and weight of YOY and yearling summer and fall walleye fingerlings and walleye of native origin (Tables 5.5 and 5.6), but the trends were not consistent across lakes. As predicted, fall fingerlings were significantly shorter and lighter as YOY than either summer fingerlings or native fish in Big Clear Lake; a similar pattern with non-significant differences was observed for yearlings in Sand (Bedford) Lake. Summer fingerlings were also significantly larger than fall fingerlings at the yearling life stage in Warrens Lake. In Flower Round Lake, no length or weight differences were apparent between the fingerling types at either the YOY or yearling life stage. Thus, summer fingerlings tended to be larger when significant differences were found. However, most of the growth comparisons were non-significant, sample sizes were generally low, and in a number of instances one of the stocking stages was not captured so a comparison could not be made.

Similar relationships in the growth patterns in walleye of native origin and summer and fall fingerlings were observed in the back-calculated length-at-age data taken from walleye that survived to the adult stage from the 1992-93 plantings. YOY walleye from Big Clear Lake were significantly smaller than YOY walleye from Sand

143

Table 5.5. Comparison of total length of native (N), summer (SF) and fall fingerlings (FF) from the 1992, 1993, and 1998 year-classes collected as YOY or yearlings. Values in parentheses are ± SE.

Lake	Capture date	Life Stage	Length (mm) (±SE)			Significance[a]
			N	SF	FF	
Big Clear	5 Oct 93	YOY	14.3 (0.2) n=12	13.9 (1.5) n=4	11.1 (0.3) n=32	*** (N,SF > FF)
Black	12-16 Nov 98	YOY	18.6 (0.5) n=6	18.3 (0.3) n=8	-	NS
Sand (Bedford)	30 Aug 93	YOY	13.0 (0.9) n=7	13.1 (0.5) n=8	-	NS
		Yearling	20.7 (1.9) n=8	18.7 (1.6) n=4	16.0 (0.5) n=8	NS
Flower Round	30 Oct 92	YOY	-	-	18.9 (0.1) n=29	-
		Yearling	-	30.0 (0.6) n=9	31.9 (1.6) n=2	NS
	24 Oct 91	YOY	17.6 (0.4) n=6	17.8 (-) n=1	-	-
		Yearling	28.1 (0.4) n=3	29.5 (0.6) n=10	29.7 (-) n=1	NS
Warrens	3-11 Nov 98	YOY	-	19.0 (0.1) n=98	-	-
	13-15 Oct 99	Yearling	-	31.1 (0.1) n=128	26.4 (0.2) n=11	*** SF > FF

[a] Starred probabilities represent $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). When significant differences between groups occurred, groups that were statistically different are separated by " > ".

Table 5.6. Comparison of the weight (g) of native (N), summer (SF) and fall fingerlings (FF) from the 1992, 1993 and 1998 year-classes collected as YOY or yearlings. Capture date and sample sizes are reported in Table 5.5.

Lake	Life Stage	Weight (g) (±SE)			Significance[a]
		N	SF	FF	
Big Clear	YOY	24.6 (1.4)	24.4 (3.4)	11.1 (0.4)	*** (N,SF > FF)
Black	YOY	60.5 (4.1)	57.2 (2.9)	-	NS
Sand	YOY	21.7 (4.5)	17.4 (2.2)	-	NS
(Bedford)	Yearling	42.0 (15.9)	60.4 (16.2)	37.8 (3.0)	NS
Flower	YOY	-	-	52.6 (1.0)	-
Round	Yearling	-	233.3 (16.6)	286.5 (49.3)	NS
	YOY	41.7 (2.5)	43.4 (-)	-	-
	Yearling	264.9 (6.7)	208.5 (12.9)	217.2 (-)	* (N > SF)
Warrens	YOY	-	59.5 (1.6)	-	-

[a] Starred probabilities represent P < 0.05 (*), P < 0.01 (**), P < 0.001 (***). When significant differences between groups occurred, groups that were statistically different are separated by " > ".

145

(Bedford) and Thirteen Island lakes ($F_{3,52} = 7.7$, $P < 0.001$), so given the low samples

sizes available from all lakes, no statistical analyses could be performed. Trend analysis

suggested that fall fingerlings that survived to adulthood were smaller than summer

fingerings and native fish at age 1, but that by age 2, no growth differences were apparent

(Figure 5.2).

The potential for size differences between fall fingerlings and either walleye

planted as summer fingerlings or native fish is illustrated in Table 5.7. Fall fingerling

walleye that were left in the hatchery for one month longer than the typical stocking date

were 4 - 10 times lighter, relative to indigenous walleye or walleye stocked as summer

fingerlings, in late-October for three consecutive years. This suggests that unless fall

fingerling growth was extremely rapid, there is generally a large pre-winter size

differential between the fingerling types.

Relative contribution and survival of summer and fall fingerlings

The relative contribution of summer and fall fingerlings from the 1992-93 year-

classes in their first two years of life was variable within and between lakes (Table 5.8).

Summer fingerlings contributed significantly more individuals to the pre-winter sample

than did fall fingerlings in two YOY assessments, while fall fingerlings were

significantly better represented in two other assessments. By the time the fish were

yearlings, the abundance of summer fingerlings was significantly higher than fall

fingerling abundance in three of four assessments. Of note is the dramatic shift in the

relationship between summer and fall fingerlings in the 1991 year class from Flower
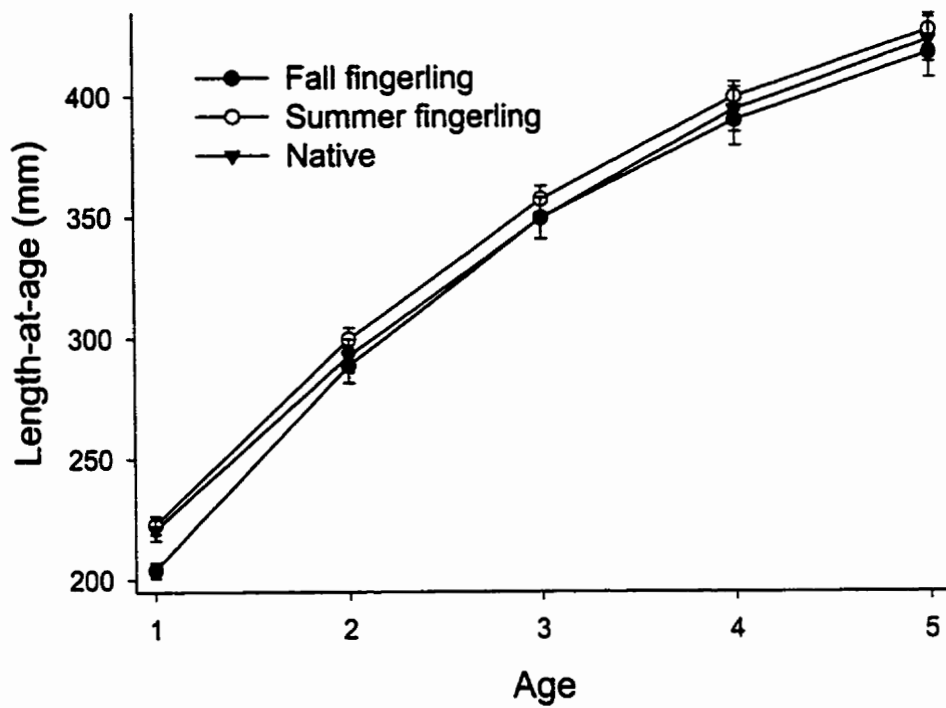
Figure 5.2. Back-calculated length-at-age in walleye stocked as summer and fall

fingerlings, relative to indigenous fish, from the combined data of Big Clear, Flower

Round, Sand (Bedford), and Thirteen Island lakes. Error bars were calculated from

individual fish and are ± standard error.

Table 5.7. Late-October weights of fall fingerling walleye in relation to summer

fingerling and indigenous walleye collected from a number of eastern Ontario lakes.

Year	Fall fingerling walleye			Native and summer fingerling walleye		
	Sample Date	weight (g) (±SE)	n	Capture Date	weight (g) (±SE)	n
1997	Oct 24	11.3 (0.3)	160	Oct 29	40.4 (4.4)	4[a]
1998	Oct 26	9.5 (0.2)	116	Oct 27-Nov 8	59.1 (1.5)	112[b]
1999	Oct 22	7.6 (0.2)	302	Oct 19-21	79.9 (3.1)	23[c]

[a] Collected from Flower Round Lake

[b] Collected from Black and Warrens lakes

[c] Collected from Black Lake

Table 5.8. Estimates of the relative contribution and survival of summer (SF) and fall fingerlings (FF) from the 1992, 1993 and 1998 year-classes at the YOY and yearling life stage. The relative survival data were determined by adjusting the relative contribution data with a 5 : 1 summer fingerling : fall fingerling stocking ratio.

Lake	Sampling date	Year class	Life stage at capture	Capture method	Relative contribution			Relative survival (SF : FF)
					SF captured	FF	Binomial probability	
Big Clear	5 Oct 93	1993	YOY	elect.	4	32	<0.001*	0.03
Black	12-16 Nov 98	1998	YOY	gill.	8	0	0.004*	-
Sand (Bedford)	30 Aug 93	1992	Yearling	elect.	4	8	0.12	0.1
Flower Round	24 Oct 91	1991	YOY	gill.	0	29	<0.001*	-
			Yearling	gill.	9	2	0.005*	0.9
	30 Oct 92	1992	YOY	gill.	1	0	0.500	-
			Yearling	gill.	10	1	0.027*	2.0
Warrens	3-11 Nov 98	1998	YOY	gill.	98	0	<0.001*	-
	13-15 Oct 99	1999	Yearling	trap.	128	11	<0.001*	2.3

Round Lake; fall fingerlings were the only stocking stage to show up in the YOY sample, but had a lower abundance than summer fingerlings in the yearling sample.

Similar patterns were observed when the relative survival of the two stages were determined for the first two years of life. The relative survival of fall fingerlings was higher in Big Clear and Flower Round lakes at the YOY life stage, while summer fingerling survival was higher for the same life stage in Warrens and Black lakes (Table 5.8). Analysis of the two fingerling sizes at the yearling stage indicated that the relative survival of fall fingerlings was higher than summer fingerlings in Sand (Bedford) Lake, and lower in Warrens and Flower Round lakes.

A consistent pattern of higher summer fingerling abundance was evident in the adult populations of the 1992-93 year classes. Two populations, Big Clear and Sand (Bedford), had significantly greater summer fingerling abundance, while the pattern was consistent but non-significant in the remaining populations (Table 5.9). This result represented a shift from the survival pattern observed in Big Clear Lake when the same fish were YOY, as at that life stage fall fingerlings significantly outnumbered summer fingerlings.

When the relative survival of the two fingerling stages was investigated after the fish had survived to the adult life stage, no significant differences in survival were observed for the three lakes tested (Student's t = 2.08, df = 2, P = 0.17; Table 5.9).

Contribution of hatchery fish to the population

Fish identified as being of hatchery origin made up large proportions of Big Clear, Flower Round, Sand (Bedford), and Thirteen Island lakes (Table 5.10). The lake with the

Table 5.9. The relative contribution and survival of summer (SF) and fall (FF)

fingerlings from the 1992-1993 year-classes in the adult stage.

| Lake | Life stage | Relative contribution | | | Relative survival (SF : FF) |
		SF	FF	Binomial Probability	
Big Clear	Adult	59	12	<0.001*	0.98
Flower Round	Adult	4	0	0.06	-
Sand (Bedford)	Adult	8	2	0.043*	0.80
Thirteen Island	Adult	7	2	0.07	0.70

Table 5.10. The relative contribution of hatchery fish to the walleye year-class of four study lakes.

Lake	Year-class	# native walleye	# stocked walleye	stocked:total (%)
Big Clear	1993	14	41	
	1992	9	16	
	1989	0	1	72.3
	1987	0	1	
	1986	0	1	
Flower Round	1993	1	2	
	1992	1	0	66.7
	1990	0	2	
Sand (Bedford)	1993	6	10	
	1992	2	0	
	1991	9	0	
	1990	1	0	41.7
	1989	2	0	
	1988	1	0	
	1987	0	4	
	1986	0	1	
Thirteen Island	1993	0	5	
	1992	1	2	
	1991	1	3	
	1990	0	1	
	1989	0	1	84.6
	1988	1	3	
	1987	0	5	
	1986	1	1	
	1985	0	1	

lowest proportion of hatchery fish still had > 40% of its population originating from hatchery stock; the highest proportion was approaching 85% hatchery fish. The data suggest that hatchery fish have become an important contributor to the adult walleye populations in these four lakes. Interestingly, the contribution of hatchery fish seemed to vary among years across lakes, as the 1987 and 1993 year-classes appeared strong and consisted primarily of hatchery fish. The relative abundance of walleye, as indicated by OMNR trapnet CUE's, declined sharply with the onset of stocking in Big Clear and Flower Round lakes, but increased substantially in Sand (Bedford) and Thirteen Island lakes (Table 5.11). The changes in relative abundance did not appear to depend on the stocking objective or pre-stocking abundance, suggesting that other factors may have influenced stocking success in these four lakes.

5.4. Discussion

The results of this study provided qualified support for the prediction that summer fingerlings would be larger than fall fingerlings prior to their first winter period. A trend towards larger summer fingerlings was apparent, but in many instances sample sizes were too low for meaningful statistical analysis. A clearer indication of the relative success of summer and fall fingerlings was obtained from the relative contribution data, as results indicated that, over the long-term, the abundance of summer walleye fingerlings was higher than that of the fall walleye fingerlings that they were pair-planted within all six of the study lakes. In addition, the results obtained from this study indicated that the relative survival of the two fingerling sizes was approximately equal. As the cost of a fall fingerling is approximately eight times that of a summer fingerling to produce (fall

Table 5.11. The relative abundance (as determined by OMNR trapnet catch-per-unit effort) of walleye captured prior to and subsequent to walleye stocking in four eastern Ontario lakes (data and stocking objectives from Seip (1995). Post-stocking CUE's were taken from the last complete OMNR netting program.

Lake	Stocking objective	Pre-stocking CUE	*Post-stocking CUE*
Big Clear	Supplemental	8.4	1.0
Flower Round	Rehabilitation	2.0	0.3
Sand (Bedford)	Put-grow-take	2.8	5.8
Thirteen Island	Rehabilitation	0.1	6.3

fingerling cost = $0.27/fish, summer fingerling cost = $0.035/fish (Seip 1995)), and no significant survival advantage was apparent for fall fingerlings, there appears to be no reason to continue stocking small waterbodies with the more expensive fall fingerlings. After 10 years of intensive stocking, hatchery individuals made up significant proportions of the populations in all of the four original study lakes. The remaining discussion will address factors capable of explaining the observed survival patterns, including size-dependent survival and potential hatchery habituation, and consider the role of walleye stocking practices on native populations.

Size differences and the potential for size-dependent mortality

Despite being larger than summer fingerlings at their respective times of stocking, I found some evidence that fall fingerlings, when they were stocked in September, were smaller than summer fingerlings or YOY of native origin that had survived to the fall. However, this relationship was not consistently observed across lakes or years, which may be partly explained by the low number of fingerlings recaptured. As such, the prediction that summer fingerlings would be larger than fall fingerlings going into the first winter was only partially supported.

Increased body size typically reduces mortality for juvenile fishes (Houde 1987, Sogard 1997); thus one might expect either summer fingerlings (as they are smaller at time of stocking) or fall fingerlings (as they are smaller going into the first winter) to face higher mortality, depending on when size-selective pressures are most intense. Mortality in YOY walleye can be high and variable throughout their first year of life, including the

155

first overwinter period (Forney 1976), so either stocking stage could be adversely affected by size-dependent processes.

At least two of the lakes involved in this study would have been predicted to favour the survival of fall fingerlings over the survival of summer fingerlings, based on the composition of their fish communities. Big Clear Lake possessed a strong native walleye population, and Thirteen Island Lake had high centrarchid densities; conditions under which size-selective mortality is expected to be intense during the summer months (Forney 1976, Santucci and Wahl 1993). As such, summer fingerlings could face a period of high mortality that fall fingerlings would not be exposed to, which would ultimately favour the establishment of the fall walleye fingerlings in those lakes. However, the relative survival to adulthood of the two fingerling types was approximately equal in both Big Clear and Thirteen Island lakes, suggesting that either summer fingerlings did not face a period of high early mortality, or if they did, that fall fingerlings had significantly lower survival rates during the first overwinter period.

Given the propensity for size-selective overwinter mortality in many YOY fishes, including walleye (Chevalier 1973, Forney 1976, Toneys and Coble 1979, Post and Evans 1989a), it was thought that pre-winter size differences would result in summer fingerlings having a size advantage that would be reflected in the observed survival patterns. As smaller fish have lower absolute energy reserves and higher weight-specific metabolic rates than their larger counterparts within a YOY cohort (Paloheimo and Dickie 1966), the first overwinter period is difficult for smaller fishes as they have to subsist primarily off their own diminishing lipid and protein reserves when feeding rates slow with the decreases in temperature. In addition, size-selective predation on the

smaller individuals of a YOY cohort has also been observed in many fishes, including walleye (Chevalier 1973, Forney 1976). As such, smaller individuals are expected to have higher overwinter mortality rates than the larger members of a cohort. I found limited evidence for pre-winter size differences in summer and fall fingerlings, but no evidence for survival differences to recruitment among the fingerling types. These results suggest that, as in Chapter 4, size-dependent overwinter mortality did not occur in the study populations. A growing body of evidence suggests that walleye populations may not be as susceptible to size-dependent overwinter mortality as other temperate species (Madenjian et al. 1996, Jonas and Wahl 1998, Copeland and Carline 1998, Chapter 4). Size-dependent overwinter mortality in walleye has primarily been attributed to cannibalism by adult walleye (Chevalier 1973, Forney 1976), and with the exception of Big Clear Lake, none of the waterbodies had abundant pre-stocking walleye populations. Thus, the apparent absence of size-dependent overwinter mortality may rest with the limited potential for cannibalism. However, I did find limited circumstantial evidence to suggest that size-selective overwinter mortality occurred in at least two of the lakes.

When the stocking events were analyzed while the walleye were still YOY, fall fingerlings were significantly more abundant than summer fingerlings in Big Clear and Flower Round lakes. The survival pattern subsequently changed in both waterbodies; in Flower Round Lake summer fingerlings significantly outnumbered fall fingerlings by the time the fish were yearlings, while in Big Clear Lake the pattern had reversed by age 4 (which was the earliest assessment after the YOY sample). There are a number of

potential explanations for the observed changes in relative abundance, one of which is that differential overwinter mortality occurred between the stocking stages.

Differential overwinter survival among fingerling types has been observed in other walleye stocking investigations (Mitzner 1992, McWilliams and Larscheid 1992). Mitzner (1992) found greater overwinter mortality for extensively reared (fish raised outdoors in ponds) fall fingerlings relative to fry stocked in the spring or intensively reared (fish raised indoors in tanks) fall fingerlings. Extensively reared fall fingerlings were smaller and in poorer condition than their intensively reared counterparts (Mitzner 1992). In addition, McWilliams and Larscheid (1992) found that the relative overwinter mortality of advanced fingerlings, equivalent to the fall fingerlings of this study, was at least twice as great as that of walleye stocked as fry. The results obtained from this study add to the growing literature that suggests the YOY life stage is not the best time to evaluate a walleye stocking event (Forney 1976, Mitzner 1992, McWilliams and Larscheid 1992). Forney (1976) determined that walleye year-class formation in Oneida Lake did not occur until walleye had successfully overwintered; he hypothesized that this was due to heavy cannibalism by older walleyes on the smaller individuals of the YOY cohort (Chevalier 1973, Forney 1976). Given that some evidence for size differences between summer and fall fingerlings going into their first winter period was detected, and that the relative contribution of summer and fall fingerlings were not established until after the first overwinter period, it is possible that size-selective overwinter mortality could explain the reversal in the relative fingerling contribution observed here.

There are alternate explanations for the observed change in survival patterns that occurred after the first overwinter period. The simplest explanation may involve the

timing of the YOY assessments. In both instances, stocked fall fingerlings had been inhabiting their respective lakes for less than two months, perhaps not allowing enough time for ecological factors to fully influence survival. However, Santucci and Wahl (1993) and Wahl (1995) showed that most predation mortality on introduced walleye occurred within a week of stocking, suggesting that anti-predatory behaviours would have already developed. Another potential explanation may include a combination of the potential differences in size and the shoaling behaviour of YOY walleye. Recent evidence suggests that like most young fishes, YOY walleye selectively shoal with similar-sized individuals (Chapter 3). Such size-assortiveness could then result in the spatial segregation of the different stocking stages, resulting in the sampling of monotypic shoals. Ultimately, if only one or two shoals are captured during a sampling period, a particular stocking stage may end up being over- or under-represented in the sample. This explanation may be particularly applicable, given the low number of fish recaptured in this study.

Another possible explanation for the apparent change in survival patterns may be the fall fingerlings long tenure under hatchery conditions. Summer fingerlings are typically stocked directly from rearing ponds just before turning piscivorous, while fall fingerlings are reared intensively on dry pellets for an additional three months. It is thought that this time spent in high density rearing tanks may inhibit the development of important feeding or anti-predatory behaviours (Gillen et al. 1981, Stein et al. 1981, Szendrey and Wahl 1995, Wahl et al. 1995), resulting in the stocking of a fish poorly adapted to its new environment.

Relatively little behavioural research has been done with hatchery walleye, though what evidence is available suggests that hatchery walleye are more likely to be successful when stocked than most other hatchery species. Walleye were less vulnerable than muskellunge (*Esox masquinongy*) to largemouth bass (*Micropterus salmoides*) predation due to their selection of vegetated habitats and close proximity to the substrate, although their ability to recognize and flee from a potential predator was poor (Wahl 1995). Hatchery walleye reared on a pellet diet also took less than a week to fully convert to piscivory and foraged at similar rates to walleye experienced in consuming live forage (Wahl et al. 1995). These results suggest that if introduced walleye can survive for about a week, they will probably acquire the behaviours necessary for short-term survival. Given that stocked walleye take a relatively long time to disperse in structurally diverse lakes (Parsons and Pereira 1997), the selection of stocking sites that can limit initial mortality becomes an important step in the ultimate success of a walleye stocking event.

The impact of stocked fish on native populations

Hatchery fish made up a large percentage of the walleye populations in Big Clear, Flower Round, Sand (Bedford), and Thirteen Island lakes. Other investigations have determined that the importance of stocked fish to populations can vary widely, with stocked fish making up 3 – 98 % of the individuals captured (McWilliams and Larscheid 1992, Lajeone et al. 1992, Mathias et al. 1992, Fielder 1992). The ability of stocked walleye to contribute to the population is believed to depend on the native year-class strength (Pereira 1987), and there is some evidence here that stocked fish contributed

160

more individuals to certain year-classes across lakes. More importantly, despite large differences in pre-stocking CUE's, stocked individuals made up large contributions to all the populations investigated here. As more evidence appears that suggests that walleye populations, and even stocks within a waterbody, are genetically distinct (e.g. Ward et al. 1989, Stepien and Faber 1998, Gatt 1998, McParland et al. 1999), it becomes more possible that important genetic variation is being lost by stocking walleye on top of existing populations. Parsons et al. (1994), Fluri (1996), and Li et al. (1996a) determined that, over the long term, stocked walleye simply replaced native individuals from the population. In addition, stocked walleye tended to suppress the year-class strength of year-classes one year younger and one year older than the stocked year-class and reduce growth rates, suggesting intraspecific interactions occur between stocked and native fish (Li et al. 1996a, Li et al. 1996b). Angling effort has also been shown to increase dramatically on lakes where stocking events occur, further depressing the stocks (Seip 1995, Johnson et al. 1996).

Determining which types of stocking events should be considered is an important concern for fishery managers. While walleye introductions have undoubtedly resulted in the development of new fisheries, evidence for success when stocking on top of existing populations remains elusive (Laarman 1978). In general, the success of most walleye plantings is low (reviews by Laarman 1978, Ellison and Franzin 1992). Big Clear Lake possessed the healthiest pre-stocking walleye population, and the stocking objective on this lake was described as supplemental (Seip 1995). Walleye abundance decreased dramatically in this lake over the course of the study, likely because publicity surrounding the stocking led to an increased number of anglers on the lake (Seip 1995).

161

In every sense, this stocking event would be considered a failure. However, walleye abundance increased on Sand (Bedford) and Thirteen Island lakes, and given the stocking objectives and low pre-stocking abundance on these lakes, these plantings would likely be considered a success in spite of any concern for the potential of genetic loss from the native populations. Thus, it is possible that stocking walleye can be used as a management tool, as long as a careful understanding of the stocking objectives and biological community are taken into consideration.

Other considerations

Given that the lakes involved in the 1992-93 stockings were planted at twice the normal OMNR stocking densities (the lakes were initially stocked with a full complement of summer fingerlings, then later stocked with a full complement of fall fingerlings), the potential for competitive effects with summer fingerlings as a factor limiting the survival of fall fingerlings should be considered. YOY walleye are affected by a number of density-dependent mechanisms (Forney 1976, Serns 1982, Hansen et al. 1998), including first year growth, which can regulate overwinter predation pressure (Chevalier 1973, Forney 1976, 1980). Recruitment can also be negatively affected by intraspecific competition (Hansen et al. 1998), so stocking fall fingerlings on top of an established population of native fish and stocked summer fingerlings may have affected the outcome of this study. However, the supposed benefit of fall fingerlings is their ability to survive in lakes where summer fingerlings are unable to establish themselves, which obviously did not occur in any of the lakes investigated here. Even if some competitive exclusion took place in the four lakes stocked in 1992-93, the fact that summer fingerlings survived

162

as well as fall fingerlings suggests the added expense of rearing walleye to the fall fingerling stage was not necessary in any case.

The results from this study clearly indicated that stocking fall fingerlings, which were larger than summer fingerlings at their respective times of stocking, for these six lakes did not increase the recruitment of individual fish. While the literature is mostly supportive that increasing size-at-stocking results in higher individual survival rates (Heidinger et al. 1985, Fielder 1992, Paragamian and Kingery 1992, Santucci and Wahl 1993, Wahl 1995), there are other studies that have found the relative contribution of smaller stocking stages to be greater than that of larger stocking stages. For example, fry were as represented as fall fingerlings most years in three Iowa lakes (Mitzner 1992, McWilliams and Larscheid 1992), and Koppelman et al. (1992) determined that small fingerlings survived better than fall fingerlings in two Missouri impoundments.

Comparing the results of this study to others is difficult due to the differences in hatchery rearing procedures, stocking densities, size-at-stocking, and stocking procedures among management agencies. For example, even the clearest of survival differences between stocking stages are not always directly comparable, due to differences in size-at-stocking. Santucci and Wahl (1993) found that large fall fingerlings survived better than medium-sized fall fingerlings, small (summer) fingerlings, or fry. However, even the medium-sized fingerlings, as defined by Santucci and Wahl (1993), were much larger than the fall fingerlings used here. It is quite possible that if the fall fingerlings were as large as those in Santucci and Wahl (1993) (>200 mm), a different outcome would have been found with this research.

The consistency of the survival to-recruitment patterns exhibited by summer and fall walleye fingerlings across six lakes and three year-classes observed in this study is unusual, given the variety of outcomes from other studies investigating the relative survival of different walleye life stages. The best example of this variability was a study by Jennings and Philipp (1992), who found that the relative survival of fry, summer fingerling, and fall fingerlings varied from year-to-year. This difference could be attributed to growth in some lakes, with faster growing life stages surviving better, but this was not true in all cases (Jennings and Philipp 1992). As well, the life stage that exhibited the fastest growth varied from year-to-year within a lake (Jennings and Philipp 1992). The variability in relative survival between stocking life stages was also apparent in other studies, such as Mitzner (1992) and McWilliams and Larscheid (1992), who showed that relative fry survival ranged from 30 - 65 % compared to 37 - 90 % for fall fingerlings. The variability inherent with these results suggests that more understanding of the mechanisms governing the early survival and ultimately the recruitment of walleye is necessary to fully understand why a stocking event succeeds or fails (Jennings and Philipp 1992). It is possible that the relatively consistent results obtained across lakes in my study have to do with the fact that all lakes were relatively small and structurally diverse, and that the study took place over a limited number of years.

There are many factors that ultimately will determine the success or failure of a stocking event, and controlling the stocking stage is only one component necessary for success. My research provides some evidence for size differences between summer and fall fingerling walleye, and the results clearly indicated that summer fingerling walleye survived as well as and contributed more individuals to the fishery than did fall

fingerlings across a variety of fish communities. Given the lower cost required to raise

summer fingerlings, I recommend that they be used in small, structurally diverse lakes

like those examined in this study when stocking is considered ecologically appropriate

and capable of achieving management objectives.

Chapter 6.

General Discussion

Size-selective mortality

Recruitment variability remains the least understood problem in all of fishery science (Houde 1987). Fishes have consistently high mortality rates during their early life stages, but a tenfold or greater variation in year-class abundance is not uncommon (Sissenwine 1984, Houde 1987, 1989). Thus, an increased understanding into the factors that influence recruitment variability is critical from an ecological and a management perspective. A current paradigm in the early life history theory of fishes is that increasing body size leads to increased survival (Sogard 1997), as mortality rates in fishes typically decrease with increasing body size (Peterson and Wroblewski 1984, Houde 1987, Miller et al. 1988). For most fishes, the greatest variation in survival occurs during the larval stage (Hjort 1914, Houde 1987). However, a number of species continue to undergo high and variable survival into the juvenile stage, where post-larval mortality can increase the variability in year-class strength (Cushing 1974, Forney 1976, Sogard 1997).

Walleye is one species where recruitment variability is believed to be primarily regulated during the juvenile stage, as variation in survival during the post-larval young-of-year stages obscured initial differences in larval abundance in Lake Oneida (Forney 1976). There are likely a number of size-dependent critical periods in the early life history of walleye, including the larval phase, during ontogenetic shifts in diet or habitat, and during the first over-winter period (Jonas and Wahl 1998). Young fishes typically face periods of high mortality, and often mortality is size-selective (Toneys and Coble

166

1979, Werner and Gilliam 1984, Post and Evans 1989a). Research suggests that first

year growth is critical to the success of walleye year-classes (Forney 1976); in particular,

successful YOY walleye year-classes depend on rapid early growth (Koonce et al. 1977,

Madenjian et al. 1996, Hansen et al. 1998). Survival was determined to be strongly size-

dependent in Lake Oneida, particularly during the overwinter period, as walleye that

reached a size of 175 mm had low overwinter mortality (Forney 1976). In addition, a

number of studies have concluded that walleye year-classes are variable until after the

first overwinter period (Forney 1976, Mitzner 1992, McWilliams and Larscheid 1992).

Thus, there is evidence that size-selective mortality is an important component of

recruitment variability for some walleye populations. Results from this dissertation,

however, were generally not supportive of the size-selective mortality paradigm.

While my research did not address the importance of rapid growth during the

larval stage, a number of researchers have concluded that size-dependent mortality likely

affects the larval stage of all fishes (Houde 1987, Miller et al. 1988). When walleye

emerge early due to rapid development, it is thought that peak larval abundance coincides

with peak zooplankton abundance. In years where walleye develop slowly, they miss the

peak plankton bloom, and are either likely to be out-competed, preyed upon, starve to

death, or be weakened to the point that they become more susceptible to predation

(Sissenwine 1984, Miller et al. 1988, Jonas and Wahl 1998). My research began

investigating the importance of size-selective mortality after the transition from being a

larval zooplanktivore to a juvenile piscivore. Immediately after becoming demersal,

walleye were located in areas of high cover and high prey density. The selection of high

cover habitats by juvenile fishes is typically thought of as a mechanism for modifying

size-selective mortality (Werner et al. 1983, Werner and Gilliam 1984), as growth rates are typically slower but survival higher in such areas (Sogard 1994). In the case of walleye, however, prey densities were also highest in the high cover areas. As rapid growth is an important component of reduced mortality rates (Houde 1987), the habitat associations of YOY walleye in Big Clear Lake during the early demersal period would suggest that they were in the unusual position of having reduced predation risk and high potential foraging rates within their preferred habitats. YOY walleye did grow quickly during the relatively short period of time they were located in the habitat types with high prey densities, reaching an average size of > 75 mm by mid-July. Thus, during an approximately one month period from mid-June to mid-July, walleye appeared to be conforming to the expectations of the size-selective mortality paradigm by maximizing growth rates.

After the early demersal period, I found little evidence that YOY walleye were conforming to the size-selective mortality paradigm. From mid-July to late fall, juvenile walleye were not residing in areas with the highest growth potential. In addition, I did not find evidence that increasing first year growth rates led to higher survival for the first over-winter period in ponds, and only limited evidence for size-selective mortality in lakes. First-year growth was also unrelated to survival in western Lake Erie, where cannibalism is rare (Madenjian et al. 1996), and in other controlled over-winter experiments (Jonas and Wahl 1998, Copeland and Carline 1998). As predation (cannibalism) did not appear to be a significant mortality factor during the over-winter survival experiment, and most of the study lakes had small populations of adult walleye, and thus low cannibalism potential, the absence of size-selective mortality may not be a

surprise. Predation by adult walleye has been proposed to explain the size-selective

mortality observed in other walleye populations (Chevalier 1973, Forney 1976,

Madenjian et al. 1991), so in the absence of cannibals size-dependent mortality may not

be in evidence, as was the case here.

The importance of size-structured interactions

The importance of body size in this dissertation was not limited to recruitment

issues. Body size was an important factor in determining which sampling technique

would provide the broadest community coverage (Chapter 2), a requirement for the

assessment of predator and prey associations in Chapter 3. In addition, changes in

walleye habitat use and shoaling behaviour appeared to depend on achieving a certain

size. Size-dependence in either case should not be a surprise, as the timing of

ontogenetic niche shifts in fishes is generally size-dependent (Werner and Gilliam 1984,

Gutreuter and Anderson 1985), while body size-assortativeness is a common component

of shoaling behaviour (Ranta et al. 1994).

Interactions between YOY walleye and other fishes undoubtedly shift during

ontogeny due to increases in body size (Werner 1988). As such, interactions are not

easily classified as predator-prey or competitive, as would be the case with piscivorous

adult walleye. The rapid change in ontogeny likely means that YOY walleye are inferior

competitors when occupying the same niche as their future prey (Werner and Gilliam

1984, Persson 1988), and may also be the basis for the suggestion that YOY walleye have

poorly developed anti-predatory behaviours (Wahl 1995). Werner and Gilliam (1984)

suggested species that grow through a series of ecological niches likely do so at a cost, by

169

reducing their competitive or anti-predatory abilities. Poor anti-predator behaviours were actually observed when snorkeling during this research, as during the stocking component of the paired-plant over 100 summer fingerling walleye were consumed within one-half hour of being stocked. Their anti-predatory response relied completely upon being cryptic and immobile, and any attempts at evasive swimming maneuvers met with little success.

The role of size-specific physiological processes and body composition was an important component of Chapter 4. Some of the predicted size-dependent relationships were not supported, and some unexpected size-specific processes were revealed. In particular, few of the expected size-dependent energetic relationships were observed, and the over-winter pattern of size-dependent weight change was opposite to that which was predicted. The diminished importance of size-dependent energetic relationships has been previously noted in walleye (Copeland and Carline 1998), suggesting that the overwinter energetic dynamics for walleye are different than those faced by some other temperate YOY fishes. In part, the absence of size-dependent energetic relationships and the lack of size-specific overwinter survival may be explained by the total size obtained by YOY walleye, as few other temperate fishes can reach > 200 mm in their first growing season. Body size may also help explain the unexpected relationship between pre-winter body weight and overwinter weight change. Smaller fishes have higher size-specific feeding and growth rates (Kamler 1992); thus, smaller fish may be able to overcome their higher metabolic costs. The size-specific feeding and growth rates also form the relationships behind the theory of ontogenetic competition, where size-specific changes in the rates of foraging and metabolism can shift the expected outcome of competitive interactions,

depending on environmental conditions (Werner 1988, 1994, Persson et al. 1998). In particular, times of high competition tend to favour smaller individuals in a cohort (Werner 1994), as smaller fish have higher foraging rates and greater growth potential than their larger counterparts (Kamler 1992).

Predator-prey interactions

Interactions between predator and prey fishes are among the most important size-dependent interactions in temperate systems (Werner et al. 1983). Predator-prey interactions have previously been identified as important in walleye recruitment variability (Forney 1976), and predator-prey dynamics were found to be important throughout this dissertation. Forney (1976) suggested that the strength of other YOY year-classes, in particular yellow perch (*Perca flavescens*), was critical to the successful transition of YOY walleye from pelagic to demersal stage, as large YOY perch numbers could provide a buffer from cannibalism. In addition, YOY yellow perch are an important food item for YOY walleye in Oneida Lake (Raney and Lachner 1942), and large perch year-classes may be important in aiding the switch to piscivory by YOY walleye that occurs during this transition. My research pointed to the further importance of prey fish in influencing the distribution of YOY walleye during the switch to piscivory, one of the critical first-year growth periods (Forney 1976, Jonas and Wahl 1998). YOY walleye were generally located in habitat types where prey densities were the highest, and prey also appeared to influence site selection at a very local level. While the importance of prey density on the distribution of YOY walleye diminished over time,

171

prey had likely already served their purpose and enabled the walleye to grow large enough to reduce the threat of predation and permit the observed habitat shift.

The importance of predation risk on YOY walleye was apparent throughout their first year of life. YOY walleye exhibited anti-predator behaviours typical of smaller fishes during the early demersal period. YOY walleye were located in areas of high cover, which reduces the foraging efficiency of piscivores (Savino and Stein 1982, Gotceitas and Colgan 1990) and are typically used by small fishes when the risk of predation is high (Werner et al. 1983, Mittelbach 1984). In addition, at small body size YOY walleye were associated with large shoals, which is also thought to be a mechanism for reducing predation risk (Pitcher 1986). Later in the summer, YOY walleye were located primarily in shallow areas, which is believed to be another important refuge area for prey fishes (Power 1984, Schlosser 1988, Angermeier 1992). During the first overwinter period, YOY walleye reared in the presence of predators had significantly lower lipid levels, lower specific energy content, and had higher weight loss than YOY walleye reared in predator-free ponds. Predators can alter metabolic rates, thereby increasing stress levels in fish (Rehnberg et al. 1987, Järvi 1989). Thus, predators may be important factors in determining the habitat selection and influencing the physical condition of walleye throughout the YOY life stage.

Sampling design and techniques

One outcome demonstrated by this research was the importance of understanding the limitations of sampling design in a research program. Gillnets and underwater visual transects produced different assessments of the same fish community across a wide range

172

of littoral zone habitats. This suggests that researchers must be careful in selecting a technique as different sampling methods can lead to variable results. Only one of the three sampling methods, the rapid visual technique (RVT), used in this research was able to successfully sample YOY walleye across a temporal scale. Straight-line visual transects rarely sampled walleye, while short-term small-mesh gillnet sets never sampled YOY walleye during the summer months. Small-mesh gillnets were more successful in the fall, as the larger size obtained by walleye at this time likely increased their probability of capture (Hamley 1975). The one technique that did successfully sample walleye from the time they first became demersal (early June) to early October was the non-linear RVT. Unfortunately, any underwater visual technique can be rendered ineffectual by poor visibility or heavy macrophyte cover (Helfman 1983); conditions that are common in many north temperate waterbodies.

It is also important to match the sampling technique selected with the broad objectives and hypotheses of the study, as the vulnerability of the species in question changes based on body size, shape, and behaviour (Hayes et al. 1996). As the goals of chapters two and three were community based and focused on a specific time period, it was not unexpected that an underwater visual method would be the most successful in sampling a broad diversity of fishes, since underwater visual methods tend to sample more species than traditional techniques (Kimmel 1985, Sanderson and Solonsky 1986). In contrast, a variety of active and passive gears would have to be utilized to follow a YOY year-class throughout its first year. Larval walleye are typically captured by trawling at various depths using larval trawls (Forney 1976, Graham and Sprules 1992). The RVT was successful in sampling YOY walleye during the early part of the demersal

life stage, but in late fall young walleye are thought to move offshore in preparation for winter (Raney and Lachner 1942, Forney 1976), meaning the viability of visual methods would likely be reduced. As such, both index trawling (in late summer) and gillnetting (in late fall) are used by the OMNR to assess YOY walleye recruitment in Ontario. Therefore, a comprehensive early life history study would require a complex sampling scheme, using a number of techniques, with the timing of each dependent on the yearly rate of walleye growth (e.g. Forney 1976).

The importance of temporal and spatial scale was not specifically addressed in any of the research chapters, but should be commented upon here. Researchers have recently become interested in understanding the importance of spatial scale on the habitat relationships of fishes, although most research has been conducted in streams or rivers (e.g. Bozek and Rahel 1992, Copp et al. 1994, Sowa and Rabeni 1995, Lammert and Allen 1999). My research examined the diurnal microhabitat use of fishes, but did not address large-scale factors (McMahon et al. 1996), the spatial arrangement of habitats present (Essington and Kitchell 1999), or possible diel shifts in habitat utilization patterns, which are common in many young freshwater fishes (e.g. Angermeier 1992, Riehle and Griffith 1993, Thurow 1997, Roussel and Bardonnet 1999). Lakes are typically more insular than lotic systems, so the importance of catchment processes on the habitat utilization patterns of lake fishes may be reduced in comparison to stream fishes. It is also important to note that only a single lake was investigated in chapters 2 and 3, meaning the results may not be applicable to other waterbodies. Such limitations are common features of most studies, but care should be made in extrapolating the results of this research across lakes or time periods.

Summary

In this dissertation, I investigated the importance of size-mediated interactions on

walleye recruitment. The life stage where the highest and most variable mortality occurs

in most fishes is the larval stage (Hjort 1914, Houde 1989), but the walleye is one species

where the period of most variable mortality is believed to occur during the post-larval

YOY life stages. Survival in young fishes is often size-specific, with larger individuals

surviving better than smaller individuals (Houde 1987). Thus, increasing growth rates is

believed to afford a survival advantage (Sogard 1997). My research demonstrated that in

Big Clear Lake, the life history strategy of post-larval YOY walleye followed the

predictions of the size-selective survival paradigm for a brief period (approximately 1

month post-larval) by residing in areas of high prey density and growing rapidly. After

this month-long window, however, there was very little support found for the size-

selective paradigm, as only limited evidence for size-selective overwinter survival in

YOY walleye was found in my pond or natural lake experiments. Predators were

suspected of playing an important role in mediating the growth rates of YOY walleye in

both early and late summer habitat selection, and predators strongly influenced the body

composition of YOY walleye during the overwinter experiments. Predators are

frequently the mechanism behind size-selective mortality in most aquatic systems, but

predator-induced size-selective mortality can be mediated by changes in habitat selection

and behaviour (Sogard 1997). Thus, I found only limited evidence to support the

contention that size-specific mortality influenced recruitment variability in post-larval

YOY walleye, given the physical and biological conditions of the lakes and ponds used in

175

this research. YOY walleye appeared aware of the threat posed by piscivorous predators,

but no evidence for size-specific mortality was found.

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Chapter 7.

Literature cited

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70:999-1007.

Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. Ecology 65:851-861.

Angermeier, P. L. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. Environmental Biology of Fishes 34:171-180.

Berg, O. K., and G. Bremset. 1998. Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. Journal of Fish Biology 52:1272-1288.

Bernard, G., and M. G. Fox. 1997. Effects of body size and population density on overwinter survival of age-0 pumpkinseeds. North American Journal of Fisheries Management 17:581-590.

Bohnsack, J. A., and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. United States Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service Technical Report 41.

Bozek, M. A., and F. J. Rahel.1992. Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analyses. Transactions of the American Fisheries Society 120:571-581.

Britton, R. H., and M.E. Moser. 1982. Size-specific predation by herons and its effect on the sex-ratio of natural populations of the mosquito fish *Gambusia affinis*. Oecologia 53:634-639.

Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish

populations. Bulletin of Marine Science 32:269-276.

Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations.

Journal of Wildlife Management 18:297-308.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363-388 *in* C.

B. Schreck and P. B. Moyle, editors. Methods for fish biology. American

Fisheries Society, Bethesda, MD.

Campbell, E. A. 1998. Predation by small walleyes on yellow perch: Effects of prey size

distribution. Transactions of the American Fisheries Society 127:588-597.

Carlander, K. D. 1982. Standard intercepts for calculating lengths from scale

measurements for some centrarchid and percid fishes. Transactions of the

American Fisheries Society 111:332-336.

Carlander, K. D. 1997. Handbook of freshwater fishery biology, volume 3. Life history

data on ichthyopercid and percid fishes of the United States and Canada. Iowa

State University Press, Ames, Iowa.

Carlstein, M. 1997. Effects of rearing technique and fish size on post-stocking feeding,

growth and survival of European grayling, *Thymallus thymallus* (L.). Fisheries

Management and Ecology 4:391-404.

Casselman, J. M. 1994. Otolith techniques for identifying and discriminating between

pond-cultured and indiginous walleye *Stizostedion vitreum* from the natural

environment. Ontario Ministry of Natural Resources.

Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida

Lake. Transactions of the American Fisheries Society 102:739-744.

Chipps, S. R., W. B. Perry, and S. A. Perry. 1994. Patterns of microhabitat use among four species of darters in three Appalachian streams. American Midland Naturalist 131:175-180.

Claramunt, R. M., and D. H. Wahl. 2000. The effects of abiotic and biotic factors in determining larval fish growth rates: a comparison across species and reservoirs. Transactions of the American Fisheries Society 129:835-851.

Clark, C. W., and M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45-75.

Connell, S. D., and M. J. Kingsford. 1998. Spatial, temporal, and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17:49-57.

Connell, S. D., M. A. Samoilys, M. P. Lincoln Smith, and J. Leqata. 1998. Comparisons of abundance of coral-reef fish: catch and effort surveys vs visual census. Australian Journal of Ecology 23:579-586.

Copeland, T. and R. F. Carline. 1998. Overwinter survival and lipid content of walleye fingerlings. North American Journal of Fisheries Management 18:383-390.

Copp, G. H., G. Guti, B. Rovny, and J. Cerny. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak flood plain of the Danube River. Environmental Biology of Fishes 40:329-348.

Craig, J. F. 1977. The body composition of adult perch, *Perca fluviatilis*, in Windermere, with reference to season changes and reproduction. Journal of Animal Ecology 46:617-632.

179

Crowder, L. B., J. A. Rice, T. J. Miller, and E. A. Marschall. 1992. Empirical and

theoretical approaches to size-based interactions and recruitment variability in

fishes. Pages 237-255 *in* Individual-based model and approaches in ecology. D. L.

DeAngelis and L. J. Gross, editors. Chapman and Hall, New York.

Cui, G., C. S. Wardle, C. W. Glass, A. D. F. Johnstone, and W. R. Mojsiewicz. 1991.

Light levels thresholds for visual reaction of mackerel, *Scomber scombrus* L., to

colored monofilament nylon gill net materials. Fisheries Research 10: 255-264.

Cushing, D. H. 1974. The possible density-dependence of larval mortality and adult

mortality in fishes. Pages 103-111 *in* The early life history of fish. J. H. S.

Blaxter, editor. Springer-Verlag, Berlin.

DeMartini, E. E., and D. Roberts. 1982. An empirical test of biases in the rapid visual

technique for species-time censuses of reef assemblages. Marine Biology 70:129-

134.

Dobush, G. R., C. D. Ankney, and D.G. Kementz. 1985. The effect of apparatus,

extraction time, and solvent type on lipid extractions of snow geese. Canadian

Journal of Zoology 63:1917-1920.

Dolloff, C. A., J. Kershner, and R. Thurow. 1996. Underwater methods. Pages 533-554 *in*

B. Murphy and D. Willis, editors. Fisheries Techniques, 2nd edition. American

Fisheries Society, Bethesda, MD.

Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by juvenile walleye as influenced by

prey morphology and behavior. Canadian Journal of Fisheries and Aquatic

Sciences 54:2618-2626.

180

Eklöv, A. G., L. A.Greenberg, and H. Kristiansen. 1994. The effect of depth on the

interaction between perch (*Perca fluviatilis*) and minnow (*Phoxinus phoxinus*).

Ecology of Freshwater Fish 3:1-8.

Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and

temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*).

Canadian Journal of Fisheries and Aquatic Sciences 54:1520-1531.

Ellison, D. G., and W. G. Franzin. 1992. Overview of the symposium on walleye stocks

and stocking. North American Journal of Fisheries Management 12:271-275.

Essington, T. E., and J. F. Kitchell. 1999. New perspectives in the analysis of fish

distributions: a case study on the spatial distribution of largemouth bass

(*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 56

(Supplement 1):52-60.

Fielder, D. G. 1992. Evaluation of stocking walleye fry and fingerlings and factors

affecting their success in lower Lake Oahe, South Dakota. North American

Journal of Fisheries Management 12:336-345.

Fluri, D. 1996. Does planting fingerling walleyes work in Northeastern Ontario? Draft

report, Ontario Ministry of Natural Resources, North Bay District.

Forney, J. L. 1975. Contribution of stocked fry to walleye fry population in New York

lakes. Progressive Fish-Culturist 37:20-24.

Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*)

population of Oneida Lake, New York, 1966-1973. Journal of the Fisheries

Research Board of Canada 33:783-792.

Forney, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating

walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York.

Journal of the Fisheries Research Board of Canada 34: 1812-1820.

Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake,

New York. New York Fish and Game Journal 27:105-141.

Fraser, D. F., and J. F. Gilliam. 1992. Nonlethal impact of predator invasion: faculative

suppression of growth and reproduction. Ecology 73:959-970.

Galligan, J. P. 1960. Winter food habits of pike-perch in Oneida Lake. New York Fish

and Game Journal 7: 146-167.

Gatt, M. H. 1998. Mitochondrial DNA diversity and anthropogenic influences in walleye

(*Stizostedion vitreum*) from Eastern Lake Huron. Masters thesis, University of

Guelph.

Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge

University Press, New York.

Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger

muskellunge on minnows and bluegills in experimental systems. Transactions of

the American Fisheries Society 110:197-209.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a

model with stream-dwelling minnows. Ecology 68:1856-1862.

Glahn, J. F., D. S. Reinhold, and P. Smith. 1999. Wading bird depredations on channel

catfish *Ictalurus punctatus* in northwest Mississippi. Journal of the World

Aquaculture Society 30:107-114.

182

Goldstein, R. M. 1978. Quantitative comparison of seining and underwater observation

   for stream fishery surveys. Progressive Fish-Culturist 40:108-111.

Gotceitas, V. 1990. Variation in plant stem density and its effects on foraging success of

   juvenile bluegill sunfish. Environmental Biology of Fishes 27:63-70.

Gotceitas, V., and P. Colgan. 1990. The effects of prey availability and predation risk on

   habitat selection by juvenile bluegill sunfish. Copeia 1990: 409-417.

Graham, D. M., and W. G. Sprules. 1992. Size and species selection of zooplankton by

   larval and juvenile walleye (*Stizostedion vitreum vitreum*) in Oneida Lake, New

   York. Canadian Journal of Zoology 70:2059-2067.

Gutreuter, S. J., and R. O. Anderson. 1985. Importance of body size to the recruitment

   process in largemouth bass populations. Transactions of the American Fisheries

   Society 114:317-327.

Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the

   littoral zone of a Michigan lake. Transactions of the American Fisheries Society

   106:545-555.

Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role

   of predator mouth width and prey body depth. Transactions of the American

   Fisheries Society 12:500-508.

Hamley, J. M. 1975. Review of gill net selectivity. Journal of the Fisheries Research

   Board of Canada 32:1943-1969.

Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998.

   Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958-

   1996. North American Journal of Fisheries Management 18:764-774.

Hansson, S., and L. G. Rudstam. 1995. Gillnet catches as an estimate of fish abundance:

A comparison between vertical gillnet catches and hydroacoustic abundances of

Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Canadian

Journal of Fisheries and Aquatic Sciences 52:75-83.

Hayes, M. L. 1983. Active fish capture methods. Pages 123-145 *in* Fisheries techniques.

L. A. Nielson and D. L. Johnson, editors. American Fisheries Society, Bethesda,

MD.

Hayes, D. B., C. P. Ferreri, and W. W. Taylor. 1996. Active fish capture methods. Pages

193-200 *in* B. R. Murphy and D.W. Willis, editors. Fisheries techniques, second

edition. American Fisheries Society, Bethesda, Maryland.

Heidinger, R. C., J. H. Waddell, and B. L. Tetzlaff. 1985. Relative survival of walleye fry

versus fingerlings in two Illinois reservoirs. Proceedings of the Annual

Conference Southeastern Association Fish and Wildlife Agencies 39:306-311.

Helfman, G. S. 1983. Underwater methods. Pages 349-369 *in* Fisheries techniques. L. A.

Nielson and D. L. Johnson, editors. American Fisheries Society, Bethesda, MD.

Helfman, G. S. 1984. School fidelity in fishes: the yellow perch pattern. Animal

Behaviour 32:663-672.

Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The diversity of fishes. Blackwell

Science, Inc., Malden, MA.

Hickford, M. J., and D. R. Schiel. 1995. Catch vs count: Effects of gill-netting on reef

fish populations in southern New Zealand. Journal of Experimental Marine

Biology and Ecology 188:215-232.

Hillman, T. W., J. W. Mullan, and J. S. Griffith. 1992. Accuracy of underwater counts of

juvenile chinook salmon, coho salmon, and steelhead. North American Journal of-

Fisheries Management 12:598-603.

Hjort, J. 1914. Fluctuations in the great fisheries of Europe. Rapport et Proces-Verbaux

des Reunions, Conseil Permanent International pour l'Exploration de al Mer 20:1-

228.

Houde, E. D., and J. L. Forney. 1970. Effects of water currents on distribution of walleye

larvae in Oneida Lake, New York. Journal of the Fisheries Research Board of

Canada 27:445-456.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American

Fisheries Society Symposium 2:17-29.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae:

temperature and implied latitudinal effects. Fishery Bulletin 87:471-495.

Hubert, W. A. 1983. Passive capture techniques. Pages 95-122 *in* Fisheries techniques. L.

A. Nielson and D. L. Johnson, editors. American Fisheries Society, Bethesda,

MD.

Hubert, W. A., and D. T. O'Shea. 1992. Use of spatial resources by fishes in Grayrocks

Reservoir, Wyoming. Journal of Freshwater Ecology 7:219-226.

Huuskonen, H., and J. Karjalainen. 1997. Predator-induced respiratory responses in

juveniles of vendace *Coregonus albula*, whitefish *C. lavaretus*, perch *Perca*

fluviatilis, and roach *Rutilus rutilus*. Environmental Biology of Fishes 49:265-

269.

Jaccard, P. 1901. Distribution de la flore alpine dans le Bassin des Dranes et dans quelques regions voisines. Bulletin Societe Vaudoise des Sciences Naturelles 37:241-272.

Järvi, T. 1989. Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and presence of predators. Environmental Biology of Fishes 26:149-152.

Järvi, T. 1990. Cumulative acute physiological stress in Atlantic salmon smolts: the effect of osmotic imbalance and the presence of predators. Aquaculture 89:337-350.

Jennings, M. J., and D. P. Philipp. 1992. Use of allozyme markers to evaluate walleye stocking success. North American Journal of Fisheries Management 12:285-290.

Jobling, M. 1995. Environmental biology of fishes. Chapman and Hall, London.

Johnson, T. B., and D. O. Evans. 1991. Behaviour, energetics, and associated mortality of young-of-the-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. Canadian Journal of Fisheries and Aquatic Sciences 48:672-680.

Johnson, B. M., M. Vogelsang, and R. S. Stewart. 1996. Enhancing a walleye population by stocking: Effectiveness and constraints on recruitment. Annales Zoologici Fennici 33:577-588.

Johnston, T. A., M. N. Gaboury, R. A. Janusz, and L. R. Janusz. 1995. Larval fish drift in the Valley River, Manitoba: Influence of abiotic and biotic factors, and relationships with future year-class strengths. Canadian Journal of Fisheries and Aquatic Sciences 52:2423-2431.

Jonas, J. L., and D. H. Wahl. 1998. Relative importance of direct and indirect effects of starvation for young walleyes. Transactions of the American Fisheries Society 127:192-205.

Jones, R. S., and M. J. Thompson. 1978. Comparison of Florida reef fish assemblages using a rapid visual technique. Bulletin of Marine Science 28:159-172.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration in spawning in Atlantic salmon, *Salmo salar*. Journal of Animal Ecology 66:425-436.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 *in* Theory and application of fish food habits. D. J. Stouder, K. Fresh, and R. J. Feller, editors. Belle W. Baruch Library in Marine Science 18, University of South Carolina Press.

Kallemeyn, L. W. 1987. Correlations of regulated lake levels and climatic factors in the abundance of young of the year walleye and yellow perch in four lakes in Voyageurs National Park. North American Journal of Fisheries Management 7:513-521.

Kamler, E. 1992. Early life history of fish: an energetics approach. Chapman and Hall, New York.

Keast, A., and J. Harker. 1977. Strip counts as a means of determining densities and habitat utilization patterns in lake fishes. Environmental Biology of Fishes 1:181-188.

Kelso, J. R. M. 1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet and temperature. Journal of the Fisheries Research Board of Canada 29:1181-1192.

Kerr, S. J., and D. E. Seip. 1994. Results of a survey of field staff on historic walleye stocking and assessment activities in Ontario. Ontario Ministry of Natural Resources, Kemptville, ON.

Kerr, S. J., B. W. Corbett, N. J. Hutchinson, D. Kinsman, J.H. Leach, D. Puddister, L. Stanfield, and N. Ward. 1997. Walleye habitat: A synthesis of current knowledge with guidelines for conservation. Percid Community Synthesis, Walleye Habitat Working Group, Ontario Ministry of Natural Resources, Peterborough, ON.

Kimmel, J. J. 1985. A new species-time method for visual assessment of fishes and its comparison with established methods. Environmental Biology of Fishes 12:23-32.

Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1900-1909.

Koppelman, J. B., K. P. Sullivan, and P. J. Jeffries, Jr. 1992. Survival of three sizes of genetically marked walleyes stocked into two Missouri impoundments. North American Journal of Fisheries Management 12:291-298.

Kraai, J. E., W. C. Provine, and J. A. Prentice. 1985. Case histories of three walleye stocking techniques with cost-to-benefit considerations. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 37:395-400.

Krause, J., J.-G. J. Godin, and D. Brown. 1996. Phenotypic variability within and
between fish shoals. Ecology 77:1586-1591.

Krebs, C. J. 1989. Ecological Methodology. Addison-Welsey Educational Publishers,
Inc., Menlo Park, California.

Laarman, P. W. 1978. Case histories of stocking walleyes in inland lakes, impoundments,
and the Great Lakes - 100 years with walleyes. Pages 254-260 *in* R.L. Kendall,
editor. Selected coolwater fishes of North America. American Fisheries Society
Special Publication (11), American Fisheries Society, Washington.

LaJeone, L. J., T. W. Bowzer, and D. L. Bergerhouse. 1992. Supplemental stocking of
fingerling walleyes in the upper Mississippi River. North American Journal of
Fisheries Management 12:307-312.

Lammert, M., and J. D. Allan. 1999. Assessing biotic integrity of streams: Effects of
scale in measuring the influence of land use/cover and habitat structure on fish
and macroinvertebrates. Environmental Management 23:257-270.

Lane, J. A., C. B. Portt, and C. K. Minns. 1996. Nursery characteristics of Great Lakes
fishes. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2338.

Larscheid, J. G. 1995. Development of an optimal stocking regime for walleyes in East
Okoboji Lake, Iowa. Pages 472-483 *in* H.R. Schramm and R.G. Piper, Jr., editors.
Uses and effects of cultured fishes in aquatic ecosystems, volume 15. American
Fisheries Society, Bethesda MD.

Larscheid, J., J. Christianson, T. Gengerke, and W. Jorgensen. 1999. Survival, growth, and abundance of pellet-reared and minnow-reared muskellunge stocked in Northwestern Iowa. North American Journal of Fisheries Management.19:230-237.

Leis, A. L., and M. G. Fox. 1996. Feeding, growth, and habitat associations of young-of-the-year walleye, *Stizostedion vitreum vitreum*, in a river affected by a mine tailings spill. Canadian Journal of Fisheries and Aquatic Sciences 53:2408-2417.

Lester, N. P., W. I. Dunlop, and C. C. Wilcox. 1996. Detecting changes in the nearshore fish community. Canadian Journal of Fisheries and Aquatic Sciences 53, Supplement 1:391-402.

Li, J., Y. Cohen, D.H. Schupp, and I. R. Adelman. 1996a. Effects of walleye stocking on population abundance and fish size. North American Journal of Fisheries Management 16:830-839.

Li, J., Y. Cohen, D.H. Schupp, and I. R. Adelman. 1996b. Effects of walleye stocking on year-class strength. North American Journal of Fisheries Management 16:840-850.

Lohr, S. C., and K. D. Fausch. 1997. Multiscale analysis of natural variability in stream fish assemblages of a Western Great Plains watershed. Copeia 1997:706-724.

Madenjian, C. P., R. M. Johnson, and S. R. Carpenter. 1991. Stocking strategies for fingerling walleyes: an individual based model approach. Ecological Applications 1:280-288.

Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996.

First-year growth, recruitment, and maturity of walleyes in western Lake Erie.

Transactions of the American Fisheries Society 125: 821-830.

Mathias, J. A., W. G. Franzin, J. F. Craig, J. A. Babaluk, and J. F. Flannagan. 1992.

Evaluation of stocking walleye fry to enhance a commercial fishery in a large,

Canadian prairie lake. North American Journal of Fisheries Management 12:209-

306.

Matthews, W. J., M. E. Power, and A. J. Stewart. 1986. Depth distribution of

Campostoma grazing scars in an Ozark stream. Environmental Biology of Fishes

17:291-297.

McIvor, C. C., and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in

a marsh fish assemblage. Ecology 69:1341-1351.

McKeown, P. E., J. L. Forney, and S. R. Mooradian. 1999. Effects of stocking size and

rearing method on muskellunge survival in Chautauqua Lake, New York. North

American Journal of Fisheries Management 19:249-257.

McMahon, T. E., A. V. Zale, and D. J. Orth. 1996. Aquatic habitat measurements. Pages

83-120 *in* B. R. Murphy and D.W. Willis, editors. Fisheries techniques, second

edition. American Fisheries Society, Bethesda, Maryland.

McParland, T. L., M. M. Ferguson, and A. P. Liskauskas. 1999. Genetic population

structure and mixed-stock analyis of walleyes in the Lake Erie-Lake Huron

corridor using allozyme and mitochondrial DNA markers. Transactions of the

American Fisheries Society 128:1055-1067.

McWilliams, R. H., and J. G. Larscheid. 1992. Assessment of walleye fry and fingerling stocking in the Okoboji Lakes, Iowa. North American Journal of Fisheries Management 12:329-335.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.

Miltner, R. J., Ross, S. W., and M. H. Posey. 1995. Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthrus*) in tidal nurseries. Canadian Journal of Fisheries and Aquatic Sciences 52: 971-982.

Miranda, L. E., and W. D. Hubbard. 1994a. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. North American Journal of Fisheries Management 14:790-796.

Miranda, L. E., and W. D. Hubbard. 1994b. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80-87.

Mittlebach, G. G. 1981. Foraging efficiency and body-size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

Mitzner, L. 1992. Evaluation of walleye fingerling and fry stocking in Rathbun Lake, Iowa. North American Journal of Fisheries Management 12:321-328.

Moyle, P .B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66:1-13.

Muotka, T., A. Maeki-Petaeys, P. Kreivi, and H. Hoegmander. 1998. Spatial associations between lotic fish, macroinvertebrate prey and the stream habitat: a multi-scale approach. Boreal Environmental Research 3:371-380.

Nelson, W. G., and E. Bonsdorff. 1990. Fish predation and habitat complexity: Are complexity thresholds real? Journal of Experimental Marine Biology and Ecology 141:183-194.

Newsome, G. E., and G. Leduc. 1975. Seasonal change of fat content in yellow perch (*Perca flavescens*) in two Laurentian lakes. Journal of the Fisheries Research Board of Canada 32:2214-2221.

Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community Eniwetok Atoll. Ecological Monographs 25:295-320.

Ogden, J. C., and J. P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. Marine Ecological Progress Series 4:97-103.

Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Palmer, K., and J. Greybill. 1986. More observations on drift diving. Freshwater catch 30:22-23.

Paloheimo, J. E., and L. M. Dickie. 1966. Food and growth of fishes: effects of food and temperature on the relation between metabolism and body weight. Journal of the Fisheries Research Board of Canada 23:869-903.

Paragamian, V. L., and R. Kingery. 1992. A comparison of walleye fry and fingerling

stockings in three rivers in Iowa. North American Journal of Fisheries

Management 12:313-320.

Parsons, B. G., D. L. Pereira, and P. D. Eiler. 1994. Evaluation of walleye fingerling

stocking in three west-central Minnesota lakes. Minnesota Department of Natural

Resources Investigational Report 425.

Parsons, B. G., and D. L. Pereira. 1997. Dispersal of walleye fingerlings after stocking.

North American Journal of Fisheries Management 17:988-994.

Peltonen, H., J. Ruuhijaervi , T. Malinen, J. Horppila, M. Olin, and J. Keto. 1999. The

effects of food-web management on fish assemblage dynamics in a north

temperate lake. Journal of Fish Biology 55:54-67.

Pereira, D. 1987. Evaluation of walleye, *Stizostedion vitreum vitreum*, fingerling

stocking. Page 19 *in* Progress report on walleye research activities. Walleye

Technical Committee, North Central Division, American Fisheries Society.

Perrow, M.R., A. J. D. Jowitt, and S. R. Johnson. 1996. Factors affecting the habitat

selection of tench in a shallow eutrophic lake. Journal of Fish Biology 48:859-

870.

Persson, L. 1988. Assymmetries in competitive and predatory interactions in fish

populations. Pages 203-218 *in* B. Ebenenmand and L Persson, editors. Size-

structured populations: ecology and evolution. Springer, Heidelberg.

Persson, L., K. Leonardsson, A. M. De Roos, M Gyllenberg, and B. Christensen. 1998.

Ontogenetic scaling of foraging rates and the dynamics of a size-structured

consumer-resource model. Theoretical Population Biology 54:270-293.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41:1117-1120.

Pine III, W. E., S. A. Ludsin, and D. R. DeVries. 2000. First-summer survival of largemouth bass cohorts: Is early spawning really best? Transactions of the American Fisheries Society 129:504-513.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. Pages 294-337 *in* The behaviour of teleost fishes. T. J. Pitcher, editor. Croom Helm, London.

Pope, K. L., M. K. Flammang, and D. W. Willis. 1996. Influence of size at stocking on survival of Saugeye in a northern-latitude impoundment. Journal of Freshwater Ecology 11:447-450.

Post, J. R., and D. O. Evans. 1989a. Experimental evidence of size-dependent predation mortality in juvenile yellow perch. Canadian Journal of Zoology 67:521-523.

Post, J. R. and D. O. Evans. 1989b. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46:1958-1968.

Power, M. E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? Ecology 65:523-528.

Rahel, F. J. 1990. The hierarchical nature of community persistence: A problem of scale. American Naturalist 136:328-344.

Raney, E. C., and E. A. Lachner. 1942. Studies of the summer food, growth and

movements of yellow pikeperch, *Stizostedion vitreum vitreum*, in Oneida Lake,

New York. Journal of Wildlife Management 6:1-16.

Ranta, E., K. Lindstrom, and A. Laurila. 1994. A theoretical exploration of antipredatory

and foraging factors promoting phenotype-assorted fish schools. Ecoscience 1:99-

106.

Rehnberg, B. G., R. J. F. Smith, and B. D. Sloley. 1987. The reaction of pearl dace

(Pisces, Cyprinidae) to alarm substance: timecourse of behavior, brain amines,

and stress physiology. Canadian Journal of Zoology 65:2916-2921.

Rice, J. A., L. B. Crowder, and K. A. Rose. 1993. Interaction between size-structured

predator and prey populations: experimental test and model comparison.

Transactions of the American Fisheries Society 122:481-491.

Riehle, M. D., and J. S. Griffith. 1993. Changes in habitat use and feeding chronology of

juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in

Silver Creek, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 50:2119-

2128.

Ritchie, B. J., and P. J. Colby. 1988. Even-odd differences in walleye year-class strength

related to mayfly production. North American Journal of Fisheries Management

8:210-215.

Rossier, O. 1997. Comparison of gillnet sampling and night visual census of fish

communities in the littoral zone of Lake Geneva, Switzerland. Archive für

Hydrobiologie 139:223-233.

Roussel, J. M., and A. Bardonnet. 1999. Ontogeny of diel pattern of stream-margin habitat use by emerging brown trout, *Salmo trutta*, in experimental channels: Influence of food and predator presence. Environmental Biology of Fishes 56: 253-262.

Rozas, L. P., and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77: 101-106.

Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Marine Ecological Progress Series 99:1-16.

Ryder, R. A. 1977. Effects of ambient light variations on behaviour of yearling, subadult and adult walleyes, *Stizostedion vitreum vitreum*. Journal of the Fisheries Research Board of Canada 34:1481-1491.

Ryder. R. A., S. R. Kerr, K. H. Loftus, and H. A Regier. 1974. The morphoedaphic index, a fish yield estimator - review and evaluation. Journal of the Fisheries Research Board of Canada 31:663-688.

Sale, P. F. 1980. The ecology of fishes on coral reefs. Oceanography and Marine Biology Annual Review 18:367-421.

Sale, P. F., and W. A. Douglas. 1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. Environmental Biology of Fishes 6:333-339.

Sanderson, S. L., and A. C. Solonsky. 1986. Comparison of a rapid visual and a strip transect technique for censusing reef fish assemblages. Bulletin of Marine Science 39:119-129.

Santucci, V. J. Jr., and D. H. Wahl. 1993. Factors influencing survival and growth of

stocked walleye (*Stizostedion vitreum*) in a centrarchid-dominated impoundment.

Canadian Journal of Fisheries and Aquatic Sciences 50:1548-1558.

Santucci, V. J. Jr., D. H. Wahl, and T. W. Storck. 1994. Growth, mortality, harvest, and

cost-effectiveness of stocked channel catfish in a small impoundment. North

American Journal of Fisheries Management 14:781-789.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass

and bluegills as influenced by simulated, submersed vegetation. Transactions of

the American Fisheries Society 11:255-266.

Savoie, P. J. 1983. Exploratory fishing for young-of-the-year walleye in the Bay of

Quinte. Lake Ontario Fisheries Unit Report, Ontario Ministry of Natural

Resources, Picton, ON.

Schneider, J. C. 1983. Experimental walleye-perch management in a small lake.

Michigan Department of Natural Resources Fisheries Research Report 1905,

Cadillac, MI.

Schlosser, I. J. 1988. Predation rates and the behavioral response of adult brassy minnows

(*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. Copeia

1988:691-697.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184,

Fisheries Research Board of Canada. Ottawa, Ontario.

Seip, D. E. 1995. An evaluation of stocking walleye fingerlings in ten eastern Ontario

lakes, 1984-1993. Ontario Ministry of Natural Resources, Southern Region

Science and Technology Transfer Unit Technical Report TR-007, Kemptville,

ON.

Serafy, J. E., R. M. Harrell, and J. C. Stevenson. 1988. Quantitative sampling of small

fishes in dense vegetation: design and field testing of portable 'popnets'. Journal

of Applied Ichthyology 4:149-157.

Serns, S. L. 1982. Influence of various factors on density and growth of age-0 walleyes in

Escanaba Lake,Wisconsin, 1958-1980. Transactions of the American Fisheries

Society 111:299-306.

Sissenwine, M. P. 1984. Why do fish populations vary? Pages 59-94 *in* R.M. May, editor.

Exploitation of Marine Communities. Springer-Verlag, Berlin.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation

of temperature effects on first year survival of small-mouth bass. Transactions of

the American Fisheries Society 109:1-34.

Shuter, B. J. and J. R. Post. 1990. Climate, population variability, and the zoogeography

of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Sogard, S. M. 1994. Use of suboptimal foraging habitats by fishes: consequences to

growth and survival. Pages 103-131 in D. J. Stouder, K. L. Fresh, and R. J. Feller,

editors. Theory and application in fish feeding ecology. Belle W. Baruch Press,

Columbia, South Carolina.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a

review. Bulletin of Marine Science 60:1129-1157.

Sowa, S. P., and C. F. Rabeni. 1995. Regional evaluation of the relation of habitat to

distribution and abundance of smallmouth bass and largemouth bass in Missouri

streams. Transactions of the American Fisheries Society 124:240-251.

Stang, D. L., and W. A. Hubert. 1984. Spatial separation of fishes captured in passive

gear in a turbid prairie Lake. Environmental Biology of Fishes 11:309-314.

Stein, R. A., R. F. Carline, and R. S. Hayward. 1981. Largemouth bass predation on

stocked tiger muskellunge. Transactions of the American Fisheries Society

110:604-612.

Stepien, C. A., and J. E. Faber. 1998. Population genetic structure, phylogeography and

spawning phylopatry in walleye (*Stizostedion vitreum*) from mitochondrial DNA

control region sequences. Molecular Ecology 7:1757-1769.

Stevens, A. G. 1990. Physical habitat preferences of walleyes in streams in Wisconsin.

M.Sc. Thesis, University of Wisconsin, Stevens Point, WI.

Szendrey, T. A., and D. H. Wahl. 1995. Effects of feeding experience on vulnerability to

predation, growth, and survival of esocids. North American Journal of Fisheries

Management 15:610-620.

Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size,

condition, and lipid content in the overwinter survival of age-0 Colorado

squawfish. Transactions of the American Fisheries Society 120:346-353.

Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout

(*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6:1-7.

Thurow, R. F., and D. J. Schill. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate bull trout abundance and size structure in a second-order Idaho stream. . North American Journal of Fisheries Management 16:314-323.

Tomas, M. V., and R. C. Haas. 1995. Recent changes in the fish community of Saginaw Bay. Pages 114-115, Proceedings of the 38th Conference of the International Association of Great Lakes Research.

Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.

Toneys, M. L., and D. W. Coble. 1980. Mortality, hematocrit, osmolality, electrolyte regulation, and fat depletion of young-of-the-year freshwater fishes under simulated condition. Canadian Journal of Fisheries and Aquatic Sciences 37:225-232.

Wahl, D .H. 1995. Effect of habitat selection and behavior on vulnerability to predation of introduced fish. Canadian Journal of Fisheries and Aquatic Sciences 52:2312-2319.

Wahl, D. H., and R. A. Stein. 1989. Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. Canadian Journal of Fisheries and Aquatic Sciences 46:2095-2103.

Wahl, D. H., L. M. Einfalt, and M. L. Hooe. 1995. Effect of experience with piscivory on foraging behavior and growth of walleyes. Transactions of the American Fisheries Society 124:756-763.

Walters, J. P., and J. R. Wilson. 1996. Intraspecific habitat segregation by smallmouth

bass in the Buffalo River, Arkansas. Transactions of the American Fisheries

Society 125:284-290.

Ward, R. D., N. Billington, and P. D. N. Hebert. 1989. Comparison of allozyme and

mitochondrial DNA variation in populations of walleye, *Stizostedion vitreum*.

Canadian Journal of Fisheries and Aquatic Sciences 46:2074-2084.

Weaver, M. J., J. J. Magnuson, and M. K. Clayton. 1993. Analyses for differentiating

littoral fish assemblages with catch data from multiple sampling gears.

Transactions of the American Fisheries Society 122:1111-1119.

Werner, E. E. 1988. Size, scaling, and the evolution of life cycles. Pages 60-81 *in* B.

Ebenenmand and L Persson, editors. Size-structured populations: ecology and

evolution. Springer, Heidelberg.

Werner, E. E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects

and responses in two anuran larvae. Ecology 75:197-213.

Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983a. Experimental tests

of optimal habitat use in fish: the role of relative habitat profitability. Ecology

64:1525-1539.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983b. An experimental

test of the effects of predation risk on habitat use in fish. Ecology 64:1540-1548.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in

size-structured populations. Annual Review of Ecology and Systematics 15:393-

496.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging

    rate-predation risk trade-off. Ecology 69:1352-1366.

Wesley, N. J., J. A. Rice, and R. L. Noble. 1999. Evaluation of two sizes of hybrid striped

    bass for introduction into small ponds. North American Journal of Aquaculture

    61:74-78.

Williamson, M. 1981. Island Populations. Oxford University Press, Oxford.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

Wright, D. I., and W. J. O'Brien. 1984. The development and field test of a tactical model

    of the planktivorous feeding of white crappie (*Pomoxis annularis*). Ecological

    Monographs 54:65-98.

Zar, J. H. 1999. Biostatistical Analysis. 4th Ed. Prentice Hall, Upper Saddle River, New

    Jersey.