

**Food Web Constraints on Chinook Salmon
Recruitment in a Large Lake Michigan Tributary**

by

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**A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Natural Resources and Environment)
in The University of Michigan
2010**

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Dedication

This dissertation is dedicated to my parents, Roger and Arlene

Acknowledgments

I would like to thank my parents, Roger and Arlene Krueger. Although it took them about 3 years to understand what I was doing as a graduate student, they have always been steadfast in their support. They always helped me through my troubles and shared in my victories. I love them very much and think the world of them. I know they are proud that my long journey toward a PhD has finally come to pass.

Thank you to my future wife, Ashley Vartoogian, who has been a great source of motivation for more than two years. I thank her for always standing by me, thinking of me, training with me, searching for post-docs, basically helping me whenever possible, especially during the last few months leading up to my defense. I love you Ashley.

Thanks to my brother and sister, Erik and Kjersten Krueger, for thinking what I do is cool, for providing some laughs along the way, and for always believing their big brother would someday finish school. I have missed them quite a bit living in Michigan the past few years while they are in Wisconsin. I thank my grandparents, Harland and Marie Watrud and the late George and Frances Krueger whom I miss dearly. They motivated me (and continue to do so) in ways they may never understand. They have been four of my biggest supporters since the day I was born. I thank my cousin and best friend, Matt, for being a constant source of motivation throughout my entire life. Thanks also to the rest of my cousins for their support and inquisitiveness. Thank you to my

aunts and uncles. They may have been confused about what my studies entailed but they still thought it sounded interesting and they were always supportive.

A huge Thank You goes out to my advisors, Dr. Edward Rutherford and Dr. Doran Mason. They took a chance bringing me to Michigan as a PhD student and I hope I made them proud. During my tenure they provided valuable direction and some great research experiences and I definitely learned a lot from them. Ed and Doran were coauthors on the main manuscripts herein (chapters 2 – 4) and their help was invaluable throughout my dissertation research and writing. Many thanks also to my committee members Dr. James Diana and Dr. Deborah Goldberg. They spent considerable time reviewing this dissertation and really helped me to improve the quality of the document. Their guidance and outside perspective on my research was very influential and definitely got me to think outside the context of fisheries management.

Lori Ivan probably deserves a bigger THANK YOU than most. We worked together for five years and there were many times where it was only the two of us sampling when the work normally required 3 or 4 people. I could not have succeeded without Lori's help. Dan Ruberg was probably the next most important person that helped me finish my field data collections. Dan was reliable and eager to learn and definitely helped to make field collections more efficient and fun. Thanks also to James Roberts, Ember Vannoy, Christine (Diana) Crissman and John Hanson for their help in the field.

I have always loved the University of Michigan so when I got a chance to get my PhD here I was very excited. The U of M School of Natural Resources and Environment was a great place to earn my PhD and I thank everyone that helped me along the way.

Finally, I could not have survived 6.5 years of dissertation work without the support of NOAA/GLERL and its staff.

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ABSTRACT

Natural reproduction of Chinook salmon now supplies half of all recruits to the Lake Michigan sport fishery but may vary greatly due to environmental variability and biotic interactions in tributary nursery areas. From 2004 to 2007, I evaluated the relative effect of predation by stocked sport fish species on Chinook salmon recruitment variability in the Muskegon River, a large Lake Michigan tributary. Together, walleye and brown trout annually consumed from 17 to 47% of available Chinook salmon parr. Although brown trout consumed large quantities of Chinook parr, I found that hatchery trout dominated walleye diets. Walleye were size-selective for small hatchery trout but prey size was independent of predator size. In general, walleye showed neutral selection for prey species although they positively selected for rainbow trout and selected against Chinook parr in some years. Brown trout consumed smaller-than-average Chinook salmon parr although prey size was also independent of predator size. Chinook parr were positively selected as prey by brown trout but only in April when parr were < 40 mm in length. The presence of alternate prey significantly influenced walleye predation on Chinook salmon parr while brown trout appeared to be limited by Chinook size. I developed a functional response model using a Type-II curve for walleyes and a Type-I curve for brown trout to varying abundances of prey. Brown trout had the greatest impact on Chinook salmon recruitment based on their feeding behavior and consumption rates. Management efforts to reduce brown trout abundance via stocking could increase

short-term survival of Chinook salmon parr by up to 31%. To assess long-term predation effects on Chinook recruitment from the Muskegon River, I used a stage-based matrix model (RAMAS Stage) parameterized with empirically-derived estimates of Chinook salmon growth, survival, abundance and fecundity. I simulated variable fry-to-smolt survival rates using 26 theoretical predator regimes and compared the results to baseline (i.e., observed) values. Only scenarios that involved removal of brown trout significantly increased long-term Chinook salmon recruitment. Based on the results of my dissertation research, I recommend elimination of brown trout stocking in all tributaries that produce Chinook salmon parr.

Chapter I

Introduction

Until recently, it was common for fisheries managers to promote single species viability in a particular system. However, exclusive management for a single species can lead to overexploitation, altered species interactions, asymmetric predation rates and reduced recruitment of non-target species. For these and other reasons, conventional single-species management often fails (Hilborn 2004). The case histories of Chesapeake Bay striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) provide prime examples of single-species management failure. The Chesapeake Bay striped bass stock was thought to be the most productive of the entire Atlantic coast (Merriman 1941). However, year classes continually failed and striped bass abundance significantly declined in the 1970s and early 1980s (Boreman and Austin; 1985; Goodyear et al. 1985; Richards and Rago 1999). The bluefish was the most harvested species in the U.S. Atlantic coast recreational fishery in the 1980s, but by the late 1990s, landings were only 20% of previous levels (Conover et al. 2003). The underlying problem in each case study was the lack of a comprehensive management plan. Failure to account for size-at-maturity, age-specific migrations, variability in recruitment, species interactions (i.e., predation and competition, spatial/temporal overlap), and habitat degradation (i.e.,

nutrition, toxins) led to reduced recruitment and subsequent overfishing of both species (Richards and Rago 1999; Conover et al. 2003).

Ecosystem-based fisheries management, including biotic and abiotic processes, may provide greater stability and therefore more sustainable ecosystem services than single-species management (Pikitch et al. 2004). Effective management must emphasize the interactions between target species and their predators, competitors, prey and humans. Further, management must consider effects of the environment and habitat on species interactions. Recent trends have moved toward multi-species, ecosystem-based approaches in forestry, agriculture and fisheries management (Matsuda and Katsukawa 2002; Latour et al. 2003) with the goal of maintaining ecosystem quality (Brodziak and Link 2002). In fisheries, the call for ecosystem-based management is generally directed towards marine environments (Hanna 1998; Chuenpagdee et al. 2006). This approach has proven beneficial, especially in the successful story of Chesapeake Bay striped bass (Field 1997; Richards and Rago 1999). Due to changes in management approach, it seems likely that bluefish may also be on the path to recovery (Conover et al. 2003; Lucena and O'Brien 2005).

The Laurentian Great Lakes provide some of the world's most important and unique freshwater resources. These lakes, along with associated tributaries and inland lakes would benefit from an ecosystem-based management approach. The Great Lakes contain numerous important fishes that provide the foundation for valuable sport and commercial fisheries. Fishery managers must therefore implement sustainable practices to protect vulnerable life stages and thereby promote long-term species viability. In many cases, management for one species may be detrimental to another. In Lake Huron,

for example, an over-stocked piscivore population and a burgeoning dreissenid mussel population resulted in a population crash of important alewife (*Alosa pseudoharengus*) prey (Dobiesz et al. 2005; Johnson et al. 2005). Reductions in forage fish abundance commonly lead to declining catch and size of targeted sport fishes (e.g., Johnson et al. 2005; Claramunt et al. 2009), which generally depend on a broad forage base. Further, forage fishes may facilitate coexistence among sport fishes by buffering competition and predation effects thereby allowing for a diverse sport fish assemblage. An effective management approach therefore requires a thorough understanding of species interactions between and among target and non-target species in the Great Lakes.

Chinook salmon (*Oncorhynchus tshawytscha*) is the primary target of the Great Lakes recreational fishery and a key predator in the pelagic food web. In 1966, fisheries managers began stocking salmon and trout to support recreational fisheries and consume non-native alewife, a nuisance competitor and predator of native fishes. Management control of the trophic interactions between salmonid predators and their prey (Stewart et al. 1981, Stewart and Ibarra 1991) has been disrupted as Chinook salmon now reproduce naturally, comprise approximately 50% of the adult salmon harvest in Lake Michigan, and their annual recruitments may vary by up to 4-fold (Seelbach 1985, Zafft 1992). Variable reproductive success of Chinook salmon can be influenced by biotic and abiotic factors.

Chinook salmon recruitment is dependent on several abiotic factors such as river temperature and discharge (Carl 1982, 1984; Seelbach 1985; Zafft 1992). River temperature affects the growth of young Chinook salmon and therefore influences the duration they are vulnerable to predation by gape-limited predators. Higher river

temperatures can lead to higher Chinook parr growth rates (Connor and Burge 2003), reducing the time that parr may be vulnerable to predation by gape-limited predators. Still, higher temperature also influences predator evacuation rates, thereby increasing consumption rates (Swenson and Smith 1973; Wahl and Nielsen 1985; He and Wurtsbaugh 1993). Large predators may therefore become a greater threat to Chinook salmon parr in warm years.

River discharge also may influence recruitment success. Extremely high river flows may erode salmon redds or wash fry out of favorable nursery areas (May et al. 2009) while low flows may increase siltation of spawning beds (Carl 1982). Bradford (1994) and Unwin (1997) reported that survival of Chinook salmon parr is positively correlated with river discharge. Elevated river flow may curb predation efficiency due to higher turbidity and the likelihood that prey will form aggregations (Petersen and DeAngelis 1992; Jager and Rose 2003). As river discharge increases, Chinook parr may be prematurely swept downstream, which reduces interactions with stream predators, thereby increasing survival in riverine habitats (Berggren and Filardo 1993). Effective dam regulations may influence Chinook parr survival through manipulation of abiotic factors (e.g., Jager et al. 1997; Jager and Rose 2003), but they also represent another source of mortality. In many Pacific Coast river systems, hydropower dams are a major determinant of Chinook smolt survival (Beamesderfer et al. 1990; Rieman and Beamesderfer 1990; Shively et al. 1996). Although abiotic factors can greatly influence Chinook survival and recruitment, they are also closely associated with biotic factors such as predation and feeding.

Biotic factors such as predation may be an even more significant source of variability for Chinook salmon recruitment compared to previously mentioned sources (Shively et al. 1996; Johnson et al. 2007). Predation from northern pikeminnow (*Ptychocheilus oregonensis*) and smallmouth bass (*Micropterus dolomieu*) can lead to high mortality rates on Chinook salmon smolts (Poe et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Fritts and Pearsons 2004) which may significantly reduce their recruitment from Pacific Coast tributaries.

Several Lake Michigan tributaries support populations of naturally reproducing Chinook salmon, but the Muskegon River is the largest source of natural recruits into Lake Michigan (Carl 1982; Johnson et al. 2005). The Muskegon River has experienced natural reproduction of Chinook salmon since the late 1970s (Carl 1982) though stocking efforts were not curtailed until 2005 (Rich O'Neal Michigan Department of Natural Resources personal communication). It is the second largest tributary (352 km; mean discharge = $62.3 \text{ m} \cdot \text{s}^{-1}$) to Lake Michigan and is a model system in which to study species interactions that may influence Chinook salmon recruitment variability.

Walleyes (*Sander vitreus*), brown trout (*Salmo trutta*), rainbow trout (*O. mykiss*) (steelhead and resident strain) and Chinook salmon are the most highly sought-after species in the Muskegon River (O'Neal 1997) and all utilize the Muskegon River as a nursery for their early life stages. Walleyes and brown trout are the most significant piscivores in the Muskegon River by size and abundance, respectively (O'Neal 1997). While brown trout are thought to prey primarily upon Chinook salmon parr, walleyes likely prey on brown trout and rainbow trout, in addition to parr (Diana 2006). Rainbow trout are approximately three times more numerous than brown trout so despite their

apparent preference for invertebrate prey, their abundance suggests they may contribute to predation mortality on Chinook salmon parr. Since walleye, brown trout and rainbow trout populations are all maintained through stocking efforts, interactions between these fishes and Chinook salmon parr may be dictated by fishery management actions. Species interactions are therefore important to quantify as they may have large implications for sport fish survival, recruitment and potential harvest.

Management actions have been shown to increase salmonid survival in west coast tributaries. Removal of northern pikeminnow in the Columbia River resulted in a large reduction in predation mortality during the smolt-to-adult stages of Coho and Chinook salmon (Rieman et al. 1991), an expected trend in heavily modified habitats (Fresh et al. 2003). Despite the increase in survival of salmon following predator removal, studies show that northern pikeminnow predation alone did not considerably reduce overall smolt-to-adult survival rates of Chinook salmon (Fresh et al. 2003). However, other species such as smallmouth bass, walleye and Caspian terns (*Sterna caspia*) added further mortality (Roby et al. 2003; Fritts and Pearsons 2004). In the Muskegon River, predation on smolts by walleye and brown trout appears to be higher and likely more significant than in west coast systems. Further, there are multiple species such as hatchery brown and rainbow trout, basses and northern pike (*Esox lucius*) that may influence Chinook recruitment through predation. Manipulation of piscivore populations has the ability to control Chinook recruitment levels through food web interactions (e.g., Beamesderfer et al. 1996; Krueger and Hrabik 2005). Therefore, it is imperative to determine the strength of various food web interactions that result from management actions on sport fisheries. The timing, location and strength of these interactions may determine the efficacy of

management in promoting future productivity of the valuable sport fisheries in the Muskegon River and other Lake Michigan tributaries.

Numerous studies have attempted to discern a more holistic approach to address the reproductive success of a target species, as well as the structure and function of the ecosystem, which includes all species present. Establishment of marine protected areas, habitat restoration and habitat creation have become popular ecosystem-based management tools for improving survival and recruitment of many riverine, lacustrine, coral reef and oceanic fishes (e.g., Martell et al. 2005; Cabaitan et al. 2008; Zeug and Winemiller 2008; Honea et al. 2009). Flow control (i.e., damming regulations) in important tributaries can be used as a means of increasing useable habitat, improving water quality and reaching desired temperatures for various fishes (e.g., Jager et al. 2003; Kiffney et al. 2009). Further, management actions that call for manipulation of fish species may lead to desired consequences for a particular fish community. These manipulations can be attempted for zooplanktivorous fishes (Søndergaard and Jeppesen 2007) or predatory fishes via changes in stocking practices (Johnson et al. 1992; Fayram et al. 2005) and changes in fishery regulations (e.g., Harvey and Kareiva 2005; Krueger and Hrabik 2005; Claramunt et al. 2009). Depending on the system, however, one approach may be more appropriate than the others.

In this dissertation, I investigated whether management actions (i.e., stocking efforts) to manipulate predator abundance could significantly impact Chinook salmon survival and recruitment. In doing so, I conducted empirical and modeling studies to quantify the effects of species interactions between Chinook salmon parr and their predators on Chinook salmon recruitment and population dynamics in the Muskegon

River, Michigan. In Chapter II, I described field surveys and diet analyses to evaluate the impact of predation by stocked sport fish species on recruitment variability of Chinook salmon in the Muskegon River. I also estimated annual abundance of Chinook salmon parr and out-migrating Chinook salmon smolts. In Chapter III, I described the feeding behavior of walleye and brown trout on variable abundances of primary and alternate forage. I further determined prey preference and/or size selection of piscivorous walleyes and brown trout and the subsequent impact on Chinook salmon recruitment in the Muskegon River. Using my estimated functional response for walleyes and brown trout, I forecasted the outcome of potential predator-prey interactions that resulted from various management manipulations. In Chapter IV, I utilized a stage-based matrix model, parameterized to approximate survival, fecundity and abundance of Chinook salmon in the Muskegon River and Lake Michigan, to model the effects of various predator-prey interaction regimes on long-term recruitment and population growth of Chinook salmon in the Muskegon River. Finally, in Chapter V, I synthesized the results of the empirical and modeling chapters and highlighted the importance of Chinook salmon recruits from the Muskegon River to the Lake Michigan adult stock.

Elucidating predator-prey interactions among important fishes may provide insight concerning management activities that are most successful in protecting and perpetuating valuable Great Lakes sport fisheries. Several important variables influence these interactions and may therefore determine the efficacy of management practices in promoting future productivity of the valuable sport fisheries in the Muskegon River and other Lake Michigan tributaries. The results of my dissertation research may therefore

provide a template for regional management of Great Lakes tributaries and similar tributaries in other regions (e.g., Pacific Northwest).

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Chapter II

Influence of Predation Mortality on Chinook Salmon Recruitment in a Lake Michigan Tributary

Abstract

Natural reproduction of Chinook salmon (*Oncorhynchus tshawytscha*) now supplies half of all recruits to the Lake Michigan sport fishery but may vary greatly due to environmental variability and biotic interactions in tributary nursery areas. From 2004 to 2007, I evaluated the relative effect of predation by stocked sport fish species on Chinook salmon recruitment variability in the Muskegon River, a large Lake Michigan tributary. In April to June of each year, I conducted electrofishing surveys and diet analysis to estimate abundance and total consumption of Chinook salmon parr by walleyes (*Sander vitreus*), brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*). Fish abundance was estimated from pass depletion methods and change in catch per unit effort while total predator consumption was quantified using a meal turnover approach. Walleye and brown trout consumed large quantities of hatchery trout and Chinook salmon, respectively. Together, these piscivores annually consumed from 18 to 49% of available Chinook salmon parr. Brown trout predation on Chinook salmon parr was largely dependent on Chinook size while walleye predation on Chinook salmon parr was largely buffered by availability of rainbow and brown trout. Therefore, vulnerability of Chinook

salmon parr to predation was likely controlled by parr growth rates and implementation of effective stocking practices for brown trout. Based on my results, fishery regulations to manipulate piscivore abundance may lead to higher survival and lower variability in naturalized Chinook salmon recruitment.

Introduction

Pacific salmon (*Oncorhynchus* spp.) were introduced into the Great Lakes in the 1960s to control overabundant alewife (*Alosa pseudoharengus*) populations and to create a sport fishery. Overall, the introduction was a success and the sport fishery now supports a multi-billion dollar annual economy (Stewart et al. 1981; Talhelm 1988). Historically, stocking hatchery-reared salmonids was essential to control alewife populations and provide a put-and-take fishery. High stocking rates and increased natural reproduction of Chinook salmon (*O. tshawytscha*) in Great Lakes tributaries, however, led to increased adult abundance, especially in Lake Michigan. The resultant increase in consumption by Chinook caused alewife to decline in abundance (Kitchell and Crowder 1986). Currently, half of all Chinook salmon recruits are naturally reproduced (Johnson et al. 2005). Hence, Chinook salmon recruitment directly influences food web dynamics in the Great Lakes themselves (Kitchell and Crowder 1986).

The Muskegon River contains one of the most productive nursery areas for wild Chinook salmon recruits in the Lake Michigan basin (Carl 1982). Average annual production of wild Chinook salmon smolts in the river nursery area is estimated near 350,000 individuals and may range from 70,000 to 700,000 (Rutherford et al. *in prep*) but smolt numbers entering the lake fishery are unknown. Combined with funding cuts, the large number of naturally produced Chinook recruits prompted fishery managers to discontinue stocking of hatchery Chinook smolts in the Muskegon River after 2005. Nonetheless, natural recruitment from the Muskegon River and other Lake Michigan tributaries remains highly variable and unpredictable (Clapp et al. 1998). While the relative magnitude of natural reproduction is generally known, there is uncertainty

regarding the factors that control production or the numbers of Chinook smolts that actually enter Lake Michigan.

Little is known regarding factors that influence the survival of juvenile Chinook salmon in river nursery habitats and during the spring out-migration in Lake Michigan tributaries. The life-history of Chinook salmon in Lake Michigan is similar to that of its oceanic source population from the Green River, Oregon (Carl 1982); spawning occurs from mid-September to early November, eggs hatch in late March and smolts out-migrate from May through June. In west coast tributaries, hydroelectric dams are responsible for smolt mortality rates of 10 - 45% per dam and predators may consume an additional 15% of salmonids (Beamesderfer et al. 1990; Rieman and Beamesderfer 1990; Shively et al. 1996). Excluding dams, predation may regulate the number of Chinook recruits emerging from the Muskegon River to Lake Michigan (e.g., Shively et al. 1996; Johnson et al. 2007), although temperature, photoperiod, and river flow are also important determinants of smoltification and out-migration timing (Carl 1982, 1984; Seelbach 1985).

The Michigan Department of Natural Resources (MDNR) discontinued Chinook salmon plantings into the Muskegon River after 2005 but continue to stock other important sport fishes that may be predators of Chinook salmon. Walleyes (*Sander vitreus*), brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*) (steelhead and resident strains) are stocked into Muskegon River nursery habitats to create a put-and-take fishery. During this time, walleyes may consume large numbers of Chinook salmon parr (e.g., Johnson et al. 2007). Walleye predation on out-migrating smolts also may depend on abundance of alternate prey including hatchery brown and rainbow trout, as well as

alewives. Thus, fishery management activities, especially stocking in the Muskegon River and Muskegon Lake, are likely to have direct effects on species interactions and wild Chinook recruitment.

I hypothesized that predation mortality is the most important source of variability in Chinook salmon recruitment in the Muskegon River. I further postulated that food web effects, resulting from management actions, have the ability to control Chinook recruitment levels through manipulation of piscivore populations (e.g., Beamesderfer et al. 1996; Krueger and Hrabik 2005). Thus, my objectives were to 1) estimate relative piscivore abundances in Muskegon River habitats; 2) determine abundance, growth and mortality of wild Chinook parr in the Muskegon River; and 3) quantify prey consumption by piscivores in the Muskegon River. I addressed these objectives using empirical data collected from 2004-2007. While other sources of mortality on Chinook salmon parr may be equal to or more important than predation, I focused on the effect of predation mortality alone because stocking of potential predators is a direct management activity that can be controlled.

Study site

The Muskegon River Estuary System (MRES) is a drowned river mouth tributary system to Lake Michigan and is located in western Michigan, USA (Figure 2.1). The MRES is composed of the Muskegon River, its associated wetlands, Muskegon Lake, and the channel connecting Muskegon Lake to Lake Michigan. The Muskegon River extends 352 km from Houghton Lake in north-central Michigan to Muskegon where it discharges into Lake Michigan. I focused my sampling on an area of Muskegon River downstream of Croton Dam, the lowermost dam on the river. Further references to the Muskegon

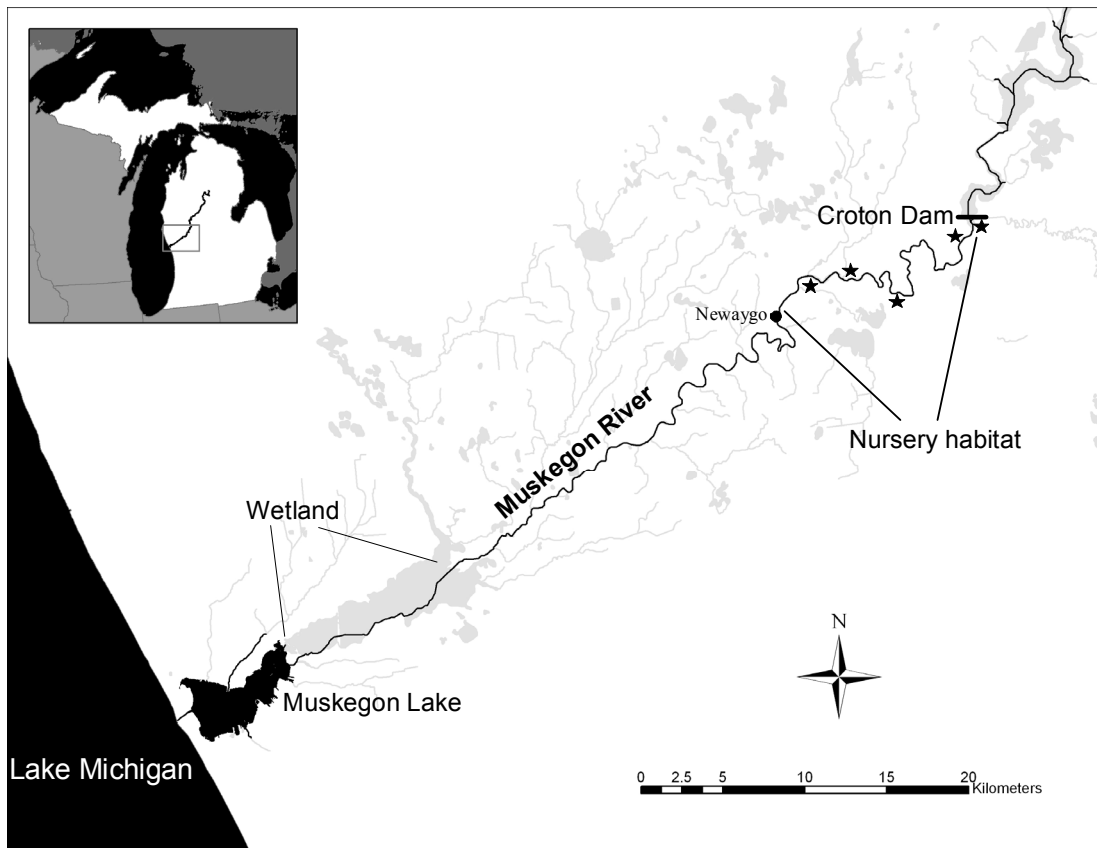


Figure 2.1. The location of the Muskegon River and Muskegon Lake, Michigan. Stars indicate barge electrofishing reference sites used to estimate population abundance of Chinook salmon parr.

River allude only to this stretch of the river. Muskegon Lake is a 1,680 hectare lake that connects to southeastern Lake Michigan via a navigation channel (Muskegon Channel). Muskegon Lake is relatively shallow and mesotrophic, with an average depth of 7.1 m (maximum 21 m) (Carter et al. 2006).

Methods

Environmental Variables

Mean daily water temperature and river discharge measurements for the upper Muskegon River were acquired from the U.S. Geological Survey station # 04121970 in Croton, Michigan. Water temperature is an important determinant of parr growth and piscivore consumption rates, while river discharge may influence feeding success, location of parr in the river and timing of smolt out-migration to Lake Michigan (Carl 1982, Seelbach 1985, Rutherford et al. *in prep*).

Fish Abundance

Chinook salmon parr

Relative abundance of Chinook salmon parr and smolts was estimated using traps and electrofishing surveys in Muskegon River from 2004 - 2007 and seines in Muskegon Lake in 2006. In 2004, I used a 2.4 m diameter auger-style smolt trap to capture out-migrating Chinook salmon parr from May 6 to June 29. Each day, Chinook salmon parr were identified, counted, weighed (nearest 0.1g) and measured (mm total length (TL)). Debris occasionally halted operations for a number of days (May 9-12, 14, 16-18, 22-26) so I linearly interpolated parr abundance from observed catches on surrounding dates. Using an average capture efficiency estimate of 3% (Rutherford et al. *in prep*), I extrapolated parr (≥ 50 mm TL) catches in the auger trap to total abundance. At 50 mm

TL, Chinook parr begin to emigrate from the Muskegon River and approach the average size at which small potential piscivores, such as hatchery raised brown and rainbow trout, are gape limited (e.g., Damsgård 1995). In 6 – 7 May 2004, 19 April – 15 June 2005, 20 April – 7 June 2006, and 8 May – 6 June 2007, I employed a barge-style electrofishing unit (3 Amps, 240V) to sample Chinook salmon parr along 100 m shoreline transects at five established reference sites (Carl 1982) (Figure 2.1). I used a three pass depletion protocol to estimate parr density (# parr \cdot m⁻¹ shoreline; e.g., Zippin 1956; 1958) because Chinook parr were generally too small to effectively mark for mark and recapture abundance estimates. I sampled each reference site twice monthly and most sites 5 times in a given field season. For each electrofishing transect I measured and weighed a subsample of 30 Chinook parr while the remaining individuals were counted and batch-weighed. I then extrapolated parr density estimates to abundance in the entire nursery area from Croton Dam to Newaygo (as defined by Godby et al. 2007) (Figure 2.1) by multiplying the mean parr density (# 100 m⁻¹) of the five reference sites by the length of the total nursery shoreline from Croton Dam to Newaygo (22.5 km x 2 sides = 45 km). I estimated the initial abundance of Chinook salmon fry by developing a linear relationship between parr length and abundance over time. I assumed that abundance at 37 mm TL (length at emergence; Beachum and Murray 1990) was initial abundance. I also calculated the peak abundance of Chinook parr larger than 50 mm for each sampling season to determine an index of potential recruitment to the Lake Michigan adult population (e.g., Carl 1984).

In 2006, I used beach seines to sample Chinook salmon smolts along the shores of Muskegon Lake and Lake Michigan from mid-May to mid-June to determine

presence/absence of Chinook salmon in Muskegon Lake and also provide a rough estimate of out-migration timing into Lake Michigan.

Predators

Relative abundance of walleye, brown trout and rainbow trout was determined using a barge electrofisher and a 20' Smith Root boom-style AC electrofishing boat. Electrical current ranged from 4-6 Amps and voltage was set to 240 V in all electrofishing transects. Spring electrofishing transects in the Muskegon River were run downstream for approximately 10 minutes and were always performed in daylight. Relative abundances of piscivores were not determined for Muskegon Lake.

The index of relative walleye abundance (CPUE, # hour⁻¹) was based on electrofishing transects and was scaled to the estimated abundance of spawning walleyes in the Muskegon River (approximately 38,000 individuals) in 2002 (Hanchin et al. 2007). Abundance of spawning walleyes was assumed to be 38,000 with walleye numbers declining as they returned to the lake. Changes in CPUE across time were scaled to initial fish abundance. Hatchery brown and rainbow trout loss rates were calculated in the same way, but initial abundance indices were based on stocking numbers for a given year.

Piscivore Diet and Consumption

Piscivore collection

Diets of piscivorous fishes from 2004 to 2007 were determined from samples collected in the Muskegon River and in Muskegon Lake using electrofishing, gillnets, and angling. In Muskegon River, fish were captured using the electrofishing methods described above. In Muskegon Lake, I used all three methods. Electrofishing transects conducted with a

20' Smith Root boom style electrofishing boat were approximately 1 km in length (~ 10 minutes) and were performed at night in shallow water (depth \leq 2 m). Upon capture, fish were placed in a 284 liter recirculating live well for the duration of a particular transect. Horizontal gill nets (3 x 30 m, 89 and 127 mm stretch mesh) were set weekly in May and June of 2005 – 2007. Gill nets were set near shore (depth 2 – 5 m) for three hours at night to minimize digestion of stomach contents and to maximize the number of fish caught. Lastly, I sampled anglers' creel at Muskegon Lake boat ramps from angling occurring at dusk or after dark.

Diet composition

Upon capture, fish were measured (TL mm), weighed (0.01 kg), and stomach contents removed. Stomach contents of live fish were flushed using a garden sprayer (e.g., Seaburg 1957) and fish were released; whole stomachs were excised from deceased fish. Diet items were qualitatively identified and recorded (when possible) in the field and then preserved in 95% ethanol or 10% formalin. In the laboratory, undigested stomach contents were separated, measured (TL mm), weighed (0.0001 g wet weight) and identified. Fish prey items were identified to species when possible, while invertebrate prey items were identified to order. Partially digested prey fish were identified based on diagnostic structures and compared to weight-at-length data of forage fish from the Muskegon River

Piscivore consumption

I used the “meal-turnover” method as described by Vigg et al. (1991) (see also Fresh et al. 2003) to quantify the daily, monthly, and total consumption of Chinook salmon parr by walleye and brown trout in the Muskegon River. In addition, I determined the

potential impact of walleye predation on stocked brown and rainbow trout abundance.

The meal-turnover approach involved identification of piscivore stomach contents, back-calculation of original prey weights, estimated state of prey digestion (based on difference in prey weight and back-calculated prey weight-at-ingestion), and prediction of time (h) to 90% evacuation of a meal for walleye. Back calculated length of digested prey was estimated from a regression of total length on the length from nape to base of tail for three common species of prey fish in the Muskegon River. Weights of prey were estimated from lengths using weight-length regressions. The equations to predict time to 90% evacuation (h in hours) for walleye (eq. 1-3; Swenson and Smith 1973; Wahl and Nielsen 1985) and brown trout were (eq. 4; He and Wurtsbaugh 1993):

$$\text{prey} < 1.1\text{g} \quad h = (-7.450 + 0.178D + 0.088R) / 0.0283T^{1.1899} \quad (1)$$

$$\text{prey } 1.1 - 2.5\text{g} \quad h = (-4.476 + 0.208D + 0.031R) / 0.0415T^{1.1899} \quad (2)$$

$$\text{prey} > 2.5\text{g} \quad h = (-0.065 + 0.231D + 0.047R) / 0.0415T^{1.1899} \quad (3)$$

$$R_e = 0.053e^{0.073T} \quad (4)$$

where D is % of prey weight digested, R is prey meal ration (g/g), T is temperature ($^{\circ}\text{C}$), and R_e is instantaneous rate of evacuation (h^{-1}) in brown trout. The number of prey consumed per predator per day was computed as the daily consumption ($\text{g} \cdot \text{day}^{-1}$) of each prey type divided by the mean mass of each prey type. A meal was defined as all diet items whose state of digestion did not vary by more than 20% (Swenson and Smith 1973). Daily consumption rates were then extrapolated to entire piscivore (walleye and brown trout) populations by multiplying daily consumption by estimates of daily abundance (e.g., Rieman et al. 1991; Vigg et al. 1991; Beamesderfer and Rieman 1991)

to determine daily, monthly and seasonal loss of Chinook salmon parr from predation, and any losses of stocked trout from walleye predation.

Chinook salmon growth

Growth rates of Chinook salmon parr were estimated from barge electrofishing collections at the five reference sites in the Muskegon River. Growth rate was estimated as the change in average parr length over time observed from bi-weekly sampling. In addition, I recorded the date at which 50% of Chinook parr measured at least 50 mm TL. The approximate time needed for parr to grow from emergence at 37 mm (Beauchum and Murray 1990) to 50 mm TL was used to determine the duration of time parr were vulnerable to small gape-limited predators (e.g., Damsgård 1995; Quinn 2005). I assumed Chinook salmon eggs were deposited on October 1, based on MDNR creel data from 2000 – 2005 (Tracey Kolb Michigan Department of Natural Resources personal communication), and used mean daily temperature to estimate the incubation time and emergence date of fry for each year, based on 1,000 accumulated thermal units (ATU) and empirical relationships between ATUs and temperature (McMichael et al. 2005). The total time that Chinook salmon parr spent in the river (i.e., swim-up to mean emigration date) also was estimated to determine temporal overlap with other piscivores that are not gape-limited by Chinook parr (i.e., walleye, basses, etc).

Fish mortality/Loss rate

Total instantaneous loss rates (Z_{total}) for Chinook salmon parr from 2005 – 2007 were estimated from the slope of a linear regression of parr density estimates against time. Parr density estimates were the average of densities at all sites within a two-day period. Since reference sites were sampled only once in 2004 (Edward Rutherford Great Lakes Environmental Research Laboratory unpublished data), I assumed the total loss rate in

2004 was equal to mean total loss rate from 2005 – 2007. Total loss rate (Z_{total}) incorporates components of predation mortality (Z_{pred}) and emigration from the river (Z_{emig}) which includes other unknown sources of mortality (e.g., Ricker 1975). I summed annual consumption estimates of predation from walleye and brown trout to estimate the percentage of the Chinook salmon parr population consumed by predators (A), and then calculated $Z_{pred} = -\log_e(1 - A)$ (Ricker 1975). I estimated Z_{emig} as the difference between Z_{total} and Z_{pred} .

I estimated the mortality rates of brown trout and rainbow trout in two ways. First, I used MDNR stocking numbers as indices of initial abundance and then estimated the total mortality rate as the slope of the regression of $\log_e(\text{CPUE})$ vs. time. Second, I used my empirical consumption model to estimate walleye consumption rates on brown or rainbow trout (predation mortality), then added angler mortality (Tracy Kolb MDNR creel data) to obtain an alternate loss rate (Predation and Mortality “PAM”) for brown trout and rainbow trout.

Results

Environmental variables

Water temperature was similar between years in the Muskegon River although in 2007 there was a brief warming period in early April (Figure 2.2). Mean water temperature from April to June was 11.4°C in 2004, 2006, and 2007 but was only 10.4°C in 2005. River discharge, however, differed between years. In 2004, the Muskegon River experienced anomalous flood conditions throughout the month of May. Mean river discharge while Chinook occupied the nursery habitat (late March - June) was the highest of all four years at 118.6 m³·sec⁻¹. In 2005, mean river discharge was low throughout the

spring and summer (mean discharge $66.4 \text{ m}^3 \cdot \text{sec}^{-1}$). Mean river discharge in 2006 and 2007 was intermediate compared to 2004 and 2005 ($88.2 \text{ m}^3 \cdot \text{sec}^{-1} \pm 2$) (Figure 2.2).

Fish abundance

Peak Chinook abundance at swim-up (“fry”) averaged 491,504 ($\pm 27,864$) individuals across all sampling years and ranged from 459,717 to 511,712 (Figure 2.3). Chinook parr $\geq 50 \text{ mm TL}$ were present by the first week of May in all years, although in 2006 they occurred as early as April 20. By the end of May, over 50% of Chinook parr captured were $\geq 50 \text{ mm TL}$ in all sampling years. Mean abundance of Chinook salmon parr $\geq 50 \text{ mm TL}$ for all years was 325,018 ($\pm 47,330$) individuals (Figure 2.4A). The mean time required for Chinook parr to reach 50mm TL, i.e., the duration of vulnerability to predation by brown trout, was 40 days and ranged from 36 to 47 days (Figure 2.4B).

Daily growth rates of Chinook salmon parr were highest in 2007 ($0.39 \text{ mm} \cdot \text{day}^{-1}$), slightly lower in 2006 ($0.36 \text{ mm} \cdot \text{day}^{-1}$) and 2004 ($0.35 \text{ mm} \cdot \text{day}^{-1}$), and lowest in 2005 ($0.30 \text{ mm} \cdot \text{day}^{-1}$). Growth rates of Chinook parr were significantly different between 2005 and 2007 ($t = 2.495$; $p = 0.025$) but were not significantly different between any other years. Chinook salmon parr successfully out-migrated from Muskegon River as I caught them in shallow, sandy areas of Muskegon Lake in late May to early June, but capture success was too low ($n = 11$) to quantify their abundance in Muskegon Lake. Mean length of out-migrant Chinook salmon parr was 60 mm and ranged from 49 to 77 mm.

The spawning population of Muskegon River walleyes ($314 \text{ mm} \leq \text{TL} \leq 810 \text{ mm}$) was estimated at nearly 38,000 (range: 30,576 – 45,203) individuals in 2002, ranging in

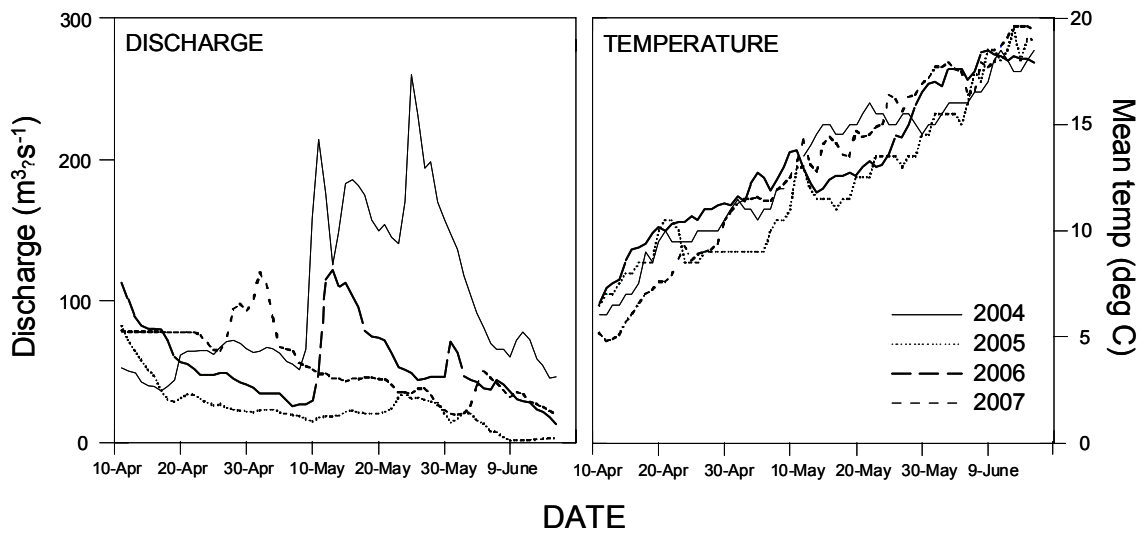


Figure 2.2. Intra- and inter-annual variation in river discharge and temperature in the Muskegon River from 2004-2007. Discharge and temperature data are only shown for the approximate duration of Chinook salmon nursery time (emergence to out-migration). Data were recorded at U.S. Geological Survey station # 04121970 in Croton, Michigan.

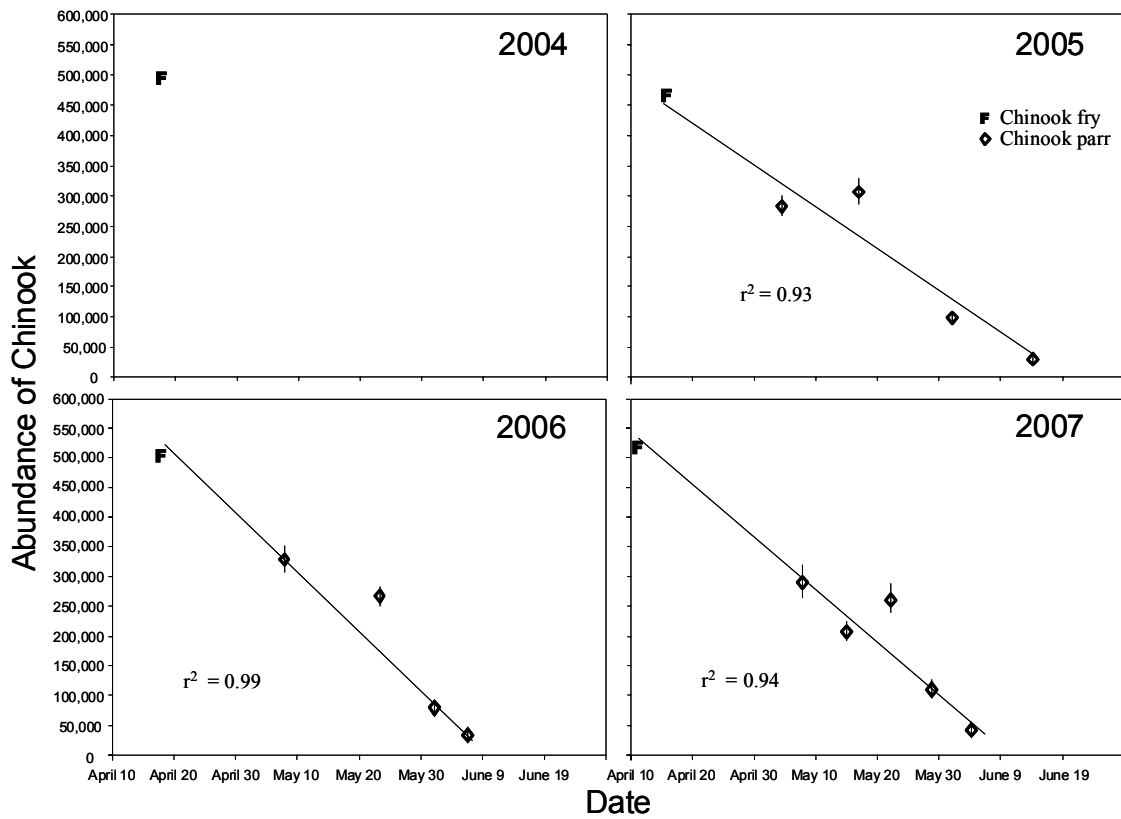


Figure 2.3. Intra- and inter-annual variation in population abundances of wild Chinook salmon fry (“F”) and parr (open diamonds; mean \pm 95% confidence intervals).

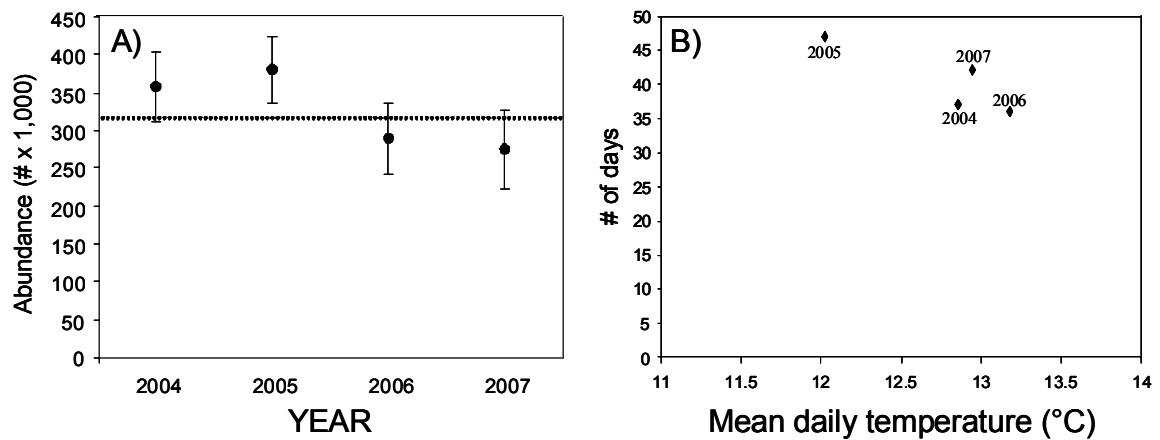


Figure 2.4. **A)** Peak abundance of Chinook salmon parr ≥ 50 mm TL. Error bars represent 95% confidence intervals; dashed line indicates the overall mean of 325,018 parr. **B)** Approximate time (days) following emergence required for 50% of Chinook parr to reach 50 mm TL in each year. Emergence date was based on an egg deposition date of October 1 and growth was dependent on mean temperature during the nursery period (swim-up to out-migration).

age from 2 to 18 years (Hanchin et al. 2007). CPUE data indicate that most walleye departed the Muskegon River immediately post-spawn, approximately April 1, but an estimated 2,000 to 3,000 adult walleye remained through June in all years (Figure 2.5). In Muskegon Lake, walleye CPUE data also showed a decreasing trend post-spawn indicating either shallow water avoidance or migration into Lake Michigan. Walleye were captured predominantly in shallow, sandy areas of Muskegon Lake in late May and early June, coincident with the location of Chinook salmon parr captured in beach seines.

Numbers of hatchery trout stocked from 2004 to 2007 were high and averaged 259,661 (mean TL = ~178 mm; Range: 140 – 217 mm TL). There was no relationship between total length of stocked trout and stocking date. Rainbow trout were stocked consistently ($189,000 \pm 11,483$) over a several week period in all study years (Figure 2.5). Brown trout stocking averaged nearly 85,000 from 2004 to 2006 but dropped by about 60% in 2007. Brown trout also were stocked over several weeks in the first three years but in 2007 were stocked in a single day (April 30) (Figure 2.5). In all years, brown trout abundance declined rapidly following stocking events and by mid June they were nearly gone (Figure 2.5). This decreasing trend was less pronounced in rainbow trout, which appeared relatively abundant throughout the sampling season (Figure 2.5).

Piscivore diet composition and consumption

I analyzed 2,096 piscivore diets (Table 2.1) collected in the MRES. Equations to back-calculate lengths of partially digested prey are reported for three common species in the Muskegon River (Table 2.2) as are weight-length regressions for five prey groups (Table 2.3). Of the walleyes examined (containing diets), 95% were piscivorous from 2004 to 2007 and consumed mainly hatchery brown and rainbow trout while in the upper

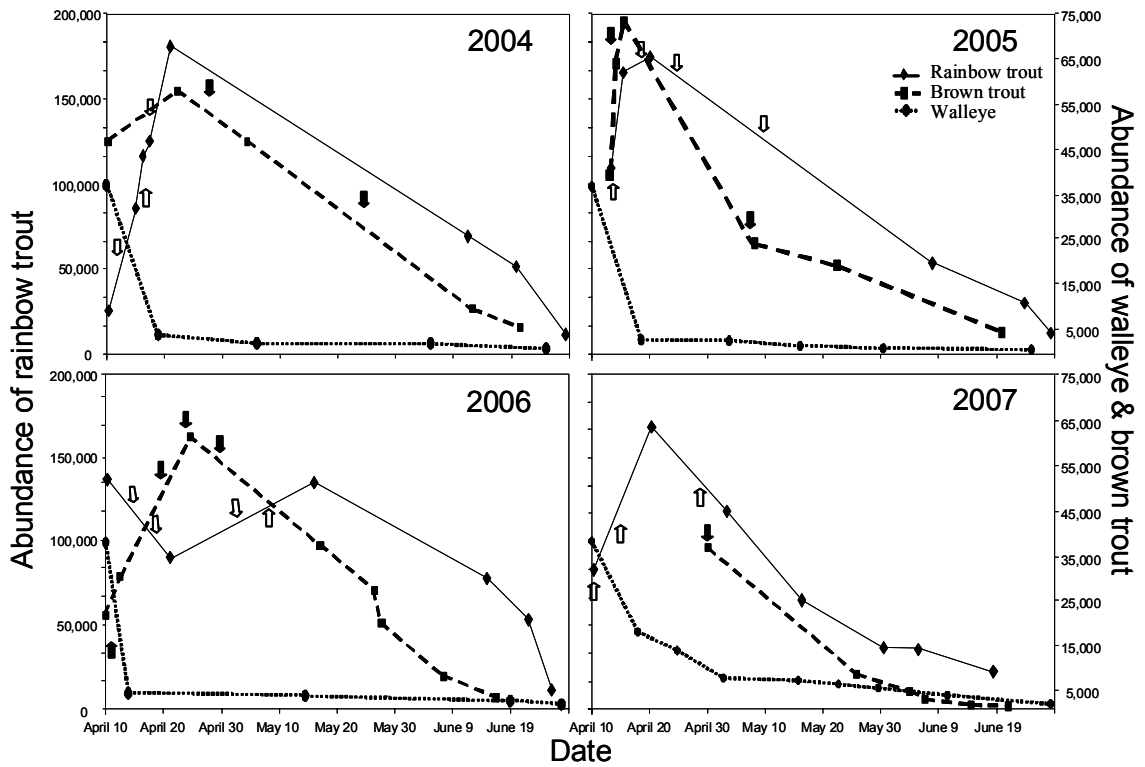


Figure 2.5. Intra- and inter-annual variation in population abundances of brown trout, rainbow trout and walleye. Filled and hollow arrows indicate stocking dates of brown and rainbow trout, respectively. Direction of arrows is arbitrary. In 2004, brown trout were also stocked on March 16 (not shown).

Table 2.1. Number of stomachs analyzed for each piscivore species. The “other” category includes bowfin (*Amia calva*), northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*) and burbot (*Lota lota*).

Year	Walleye	Brown trout	Rainbow Trout	Smallmouth Bass	Other*
2004	238	0	0	25	11
2005	371	33	52	20	11
2006	155	184	180	106	55
2007	250	73	238	81	13
Total	1,014	290	470	232	90

Table 2.2. Linear regression model ($Y = a + bX$) statistics for total length (Y) regressed on length of nape-to-base-of-tail (X) for 3 species of prey fish in the Muskegon River. All lengths are in millimeters.

Nape to base of tail				
Prey species	n	a	b	r²
Chinook salmon	98	7.1333	1.3	0.99
rainbow trout	53	20.249	1.3742	0.94
brown trout	34	10.004	1.1607	0.95

Table 2.3. Power regression model ($Y = aX^b$) statistics for weight (Y, g) regressed on total length (X, mm) for 3 prey species (and 2 groups) in the Muskegon River. The “other” category is mostly darters (*Etheostoma* spp.).

Prey species	Length range		Regression	Statistic	
	n	(mm)	a	b	r ²
Chinook parr	456	35 – 99	4.0×10^{-7}	3.7165	0.87
rainbow trout	322	83 – 220	6.0×10^{-6}	3.0848	0.97
brown trout	176	113 – 220	8.0×10^{-6}	3.0714	0.88
Cyprinidae	305	31 – 116	8.0×10^{-6}	3.0114	0.85
other fish species	70	38 – 116	1.0×10^{-5}	2.9395	0.88

Muskegon River, especially in April and May (85-90% of total biomass) (Figure 2.6). Chinook salmon parr, on the other hand, only comprised about 0.1 to 15% of the biomass of walleye seasonal diet (Figure 2.6). In the lower Muskegon River, walleyes consumed primarily Cyprinidae but the proportion of Chinook salmon parr in walleye diets increased in June. In Muskegon Lake, walleye diets were dominated by abundant prey items such as alewife and gizzard shad (*Dorosoma cepedianum*) (Table 2.4). I found no evidence of walleye consuming Chinook parr in Muskegon Lake despite their spatial overlap.

Walleye consumption rates by number were higher for Chinook salmon parr than for brown trout or rainbow trout. In May, mean daily consumption rate by walleye (# prey.predator⁻¹.day⁻¹) of Chinook salmon parr was highest (2.45 parr . walleye⁻¹) in the upper Muskegon River and zero in the lower river. In June, walleye consumption of Chinook parr declined slightly in the upper river (to 2.17 parr . walleye⁻¹) and increased in the lower Muskegon River (to 1.67 parr . walleye⁻¹). Walleye consumption of brown trout was highest in May (0.31 brown trout . walleye⁻¹) although consumption of rainbow trout was always higher than of brown trout, especially in April (0.57 brown trout . walleye⁻¹). In all years, rainbow trout appeared to be the preferred forage item for walleye (Table 2.5).

Approximately 40% of stocked brown trout sampled were piscivorous and most preyed upon Chinook parr from 2005 – 2007. I found Chinook salmon parr in brown trout diets in April, immediately after brown trout were stocked, but consumption of Chinook salmon parr ceased around May 24 in each year. Brown trout diet composition (by biomass) was approximately 40% Chinook salmon parr in April and May from 2005

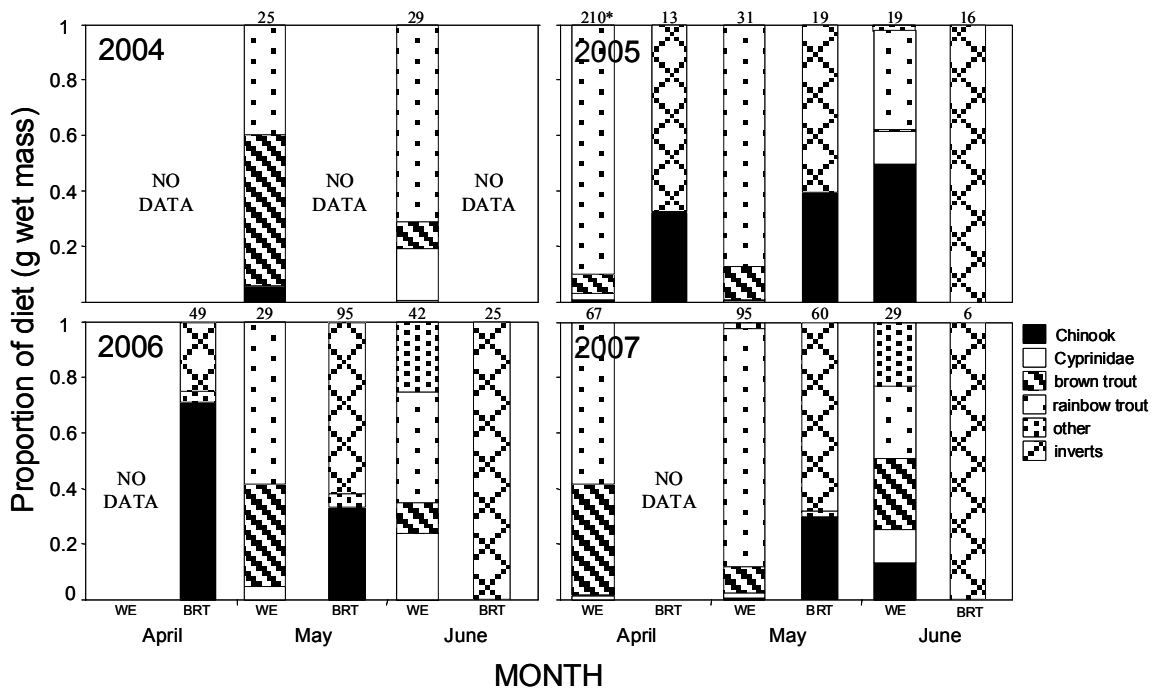


Figure 2.6. Diet composition (by mass) of walleye (“WE”) and brown trout (“BRT”) from 2004 to 2007 in the upper Muskegon River. The “other” category is composed mostly of northern pike (*Esox lucius* in walleye diets) and YOY rainbow trout (in brown trout diets). Sample sizes are listed above each column. The high sample size in April 2005 (*) was due to the capture of spawning walleye, most of which (189) did not contain diets.

Table 2.4. Diet proportions (by wet mass) for Muskegon Lake walleyes (n = 463) during 2004 – 2007. The “other” category is mostly round goby *Neogobius melanostomus*.

Month	alewife	Cyprinidae	gizzard shad	other	Chinook parr
May	0.70	0.19	0	0.11	0
June	1.00	0	0	0	0
July	0.77	0.21	0	0.02	0
August	0	0.11	0.89	0	0

Table 2.5. Mean daily consumption (# prey/predator) by walleye and brown trout on three prey species in the upper and lower Muskegon River from April to June 2004 – 2007. The number of diets listed (n) represents the total number of stomachs containing a particular diet item. The “Total” shows the number of diets as a proportion of the total number of stomachs examined.

Prey species	N	Walleye			N	Brown trout		
		April	May	June		April	May	June
Chinook parr								
upper river	36	0.150	2.453	2.168	64	1.416	1.028	0
lower river	22	0	0	1.674	0	0	0	0
brown trout								
upper river	52	0.224	0.310	0.223				
lower river	2	0	0	0.017				
rainbow trout								
upper river	157	0.569	0.482	0.390				
lower river	7	0	0	0.087				
Total	276 / 1014			64 / 290				

to 2007 (Figure 2.6). Consumption of Chinook parr by brown trout from 2005 to 2007 was higher than by walleye in April and May but lower in June (Figure 2.7). Brown trout mean daily consumption of Chinook salmon parr was highest in April at approximately $1.42 \text{ Chinook} \cdot \text{predator}^{-1} \cdot \text{day}^{-1}$, was 38% lower in May, and by June all brown trout were insectivorous. Approximately 38% of brown trout consumed Chinook salmon parr in 2007 (highest), 33% in 2005 and 26% in 2006 (mean 30%).

Predation on Chinook salmon parr by other fish species was negligible. Rainbow trout did not consume Chinook salmon parr to an appreciable degree; nearly all rainbow trout diets were composed exclusively of invertebrates (mainly *Trichoptera* and *Ephemeroptera* spp.). Although I collected diet samples from other piscivorous species, most notably smallmouth bass, they did not consume Chinook salmon parr in appreciable amounts and therefore were not considered in the subsequent analyses.

Average annual consumption of Chinook salmon parr by walleye over all years was lower (46,809 parr) than by brown trout. Walleye consumed approximately 91,288 and 71,191 Chinook salmon parr in the spring of 2004 and 2005, respectively (Figure 2.8). In 2007, however, they only consumed 24,824 Chinook salmon parr and in 2006 seasonal consumption of Chinook parr by walleye was nearly absent (934 parr). Brown trout consumed an estimated 174,278 and 131,100 Chinook salmon parr in 2005 and 2006, respectively, but only consumed 77,516 Chinook parr in 2007 (Figure 2.8).

Mortality/loss rates

Predation mortality was likely a large component of total loss rates for Chinook salmon parr. Total instantaneous daily loss (Z_{total}) rates for Chinook parr averaged 0.058 and

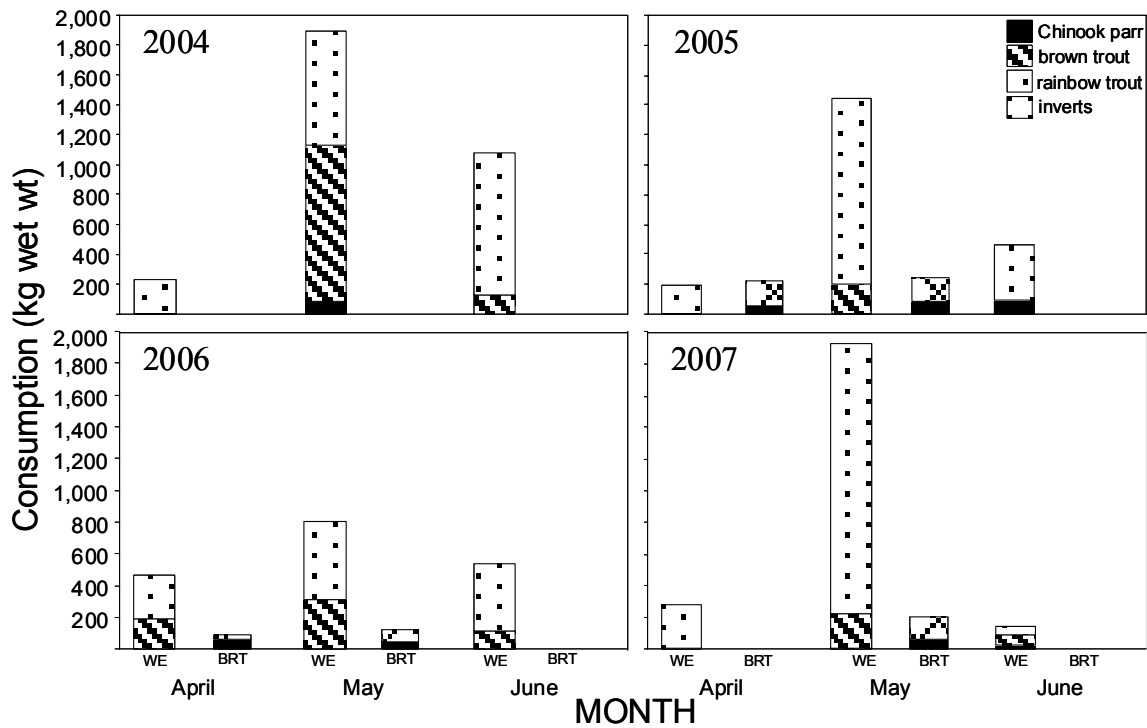


Figure 2.7. Monthly consumption for brown trout (“BRT”) and walleye (“WE”) on the most common prey items from 2004 to 2007. Brown trout diet data were not available for 2004.

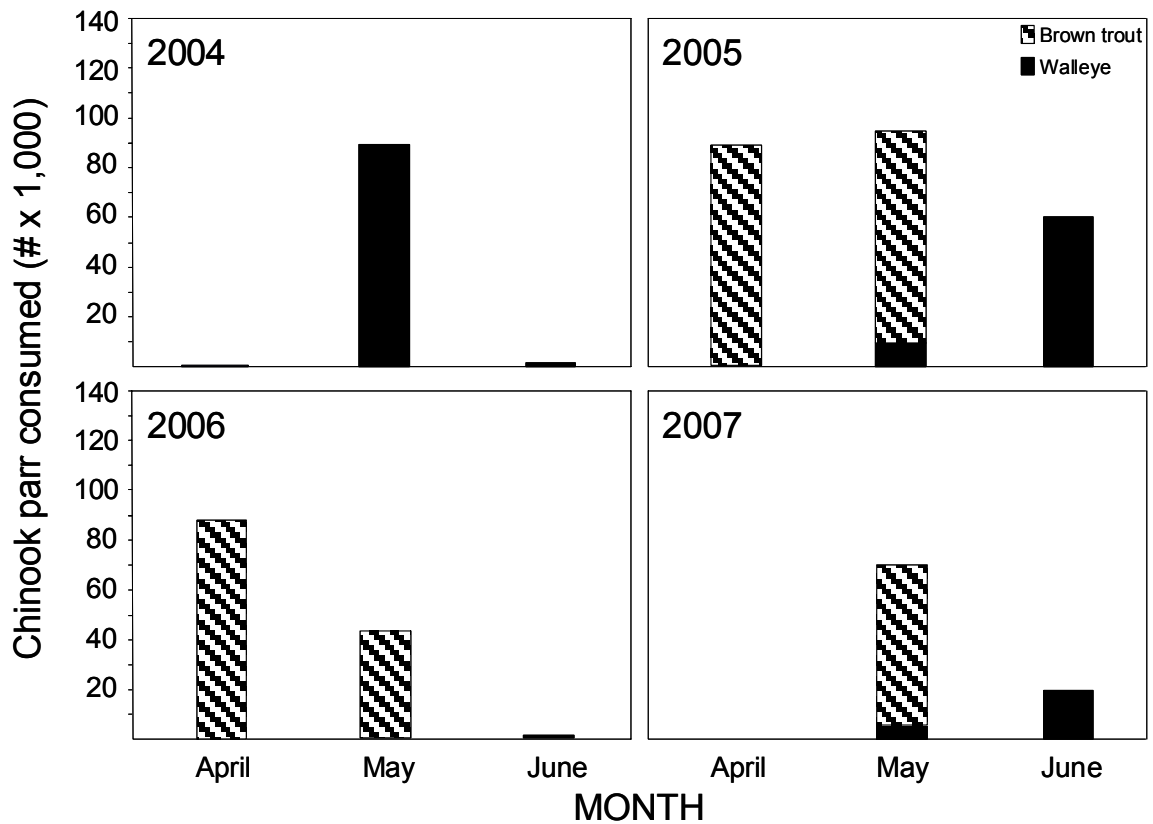


Figure 2.8. Total number of Chinook salmon parr consumed by walleye (solid bars) and brown trout (hatched bars) from 2004 to 2007 based on the empirical consumption model. Brown trout diet data were not available for 2004.

ranged from 0.052 to 0.077 (Table 2.6). Mean instantaneous daily predation mortality ($Z_{pred} = -\log_e (1 - A)$), however, also was highest in 2005 (0.0139) but lowest in 2006 (0.0068). Peak predation mortality on Chinook salmon parr by walleye was estimated at 18% of initial abundance (2004) (Table 2.6). Stocked brown trout appeared to consume higher proportions of Chinook parr than did walleye and most predation mortality was attributed to brown trout (Table 2.6). Peak predation mortality owing to brown trout was 34% (2005) and total predation mortality by both species on Chinook parr peaked at 49%, also in 2005. Based on the estimates of predation mortality (% mortality), the percentage of wild-produced Chinook salmon parr that emigrated (or experienced mortality from other sources) as smolts from the Muskegon River ranged from 27% in 2005 (124,124 smolts) to 80% in 2007 (409,370 smolts) (Table 2.6).

Angling mortality on brown trout and rainbow trout in the Muskegon River was low compared to predation mortality by walleye. Brown trout and rainbow trout harvests averaged 2.5% and 9% of numbers stocked, respectively, from 2000 to 2005. Walleye predation mortality averaged 11% for brown trout and 11.4% for rainbow trout (Table 2.6). Date-specific estimates of brown trout abundance based on CPUE data (i.e., Z_{total}) were on average 35% lower than the numbers consumed by predators and harvested by anglers, suggesting significant loss rates of brown trout due to emigration.

Discussion

Interactive effects of abiotic variables, predators and alternate prey

It is difficult to discern the relative effect of abiotic (i.e., river flow, water temperature) versus biotic factors (i.e., predation and competition) in empirical studies. For example,

Table 2.6. Instantaneous daily loss rates ($Z \cdot d^{-1}$) of Chinook salmon parr, brown trout, rainbow trout and walleyes in the Muskegon River from 2004 to 2007. Total loss rates (Z_{total}) were estimated as regression slopes of abundance over time; Losses due to consumptive predation were estimated by daily ration estimates, and for anglers through MDNR creel surveys. Losses due to emigration (Z_{emig}) were estimated as $Z_{total} - Z_{pred}$. No data were available (n.a.) on brown trout consumption of Chinook salmon parr in 2004. Creel data were not available for 2006 and 2007 so mean values from 2000 to 2005 were used.

Prey	Z_{total}	Z_{pred}		Z_{emig}	mortality via predation & angling	# emigrated smolts
Chinook		Brown trout	Walleye			
2004	n.a.	n.a.	0.0026	n.a.	0.18	n.a.
2005	0.045	0.011	0.0031	0.0309	0.49	124,124
2006	0.077	0.0081	0.0001	0.0689	0.26	286,758
2007	0.052	0.0044	0.0009	0.0467	0.20	409,370
Brown Trout		Anglers	Walleye			
2004	0.018	0.00017	0.0025	0.015	0.22	
2005	0.02	0.0001	0.0004	0.0195	0.05	
2006	0.04	0.00015	0.0011	0.0388	0.12	
2007	0.074	0.00015	0.003	0.07	0.14	
Rainbow Trout		Anglers	Walleye			
2004	0.007	0.0002	0.0025	0.0043	0.25	
2005	0.017	0.0003	0.0023	0.0144	0.25	
2006	0.009	0.00028	0.0016	0.007	0.21	
2007	0.015	0.00028	0.0018	0.013	0.22	

while higher river temperatures can lead to higher growth rates of Chinook parr (Connor and Burge 2003), higher temperatures also influence predator consumption, thereby increasing parr vulnerability to predation (e.g., Marine and Cech 2004). Survival of Chinook salmon parr is positively correlated with river discharge (Unwin 1986; Bradford 1994; Smith et al. 2003). Premature emigration may reduce interactions with stream predators, thereby increasing survival in riverine habitats. In the Muskegon River in 2005, mean temperature and mean river discharge were the lowest of all sampling years and corresponded to the lowest fry production and the highest rates of predation mortality from walleye and brown trout. In 2006 and 2007, mean water temperature and mean river discharge were significantly higher than in 2005 and corresponded to an increase in fry production and a substantial reduction in Chinook predation mortality in 2007, but not in 2006. Despite the potential influence of river temperature and discharge, it was difficult to determine how much temperature and flow directly influenced Chinook parr survival since abiotic factors are highly correlated, and directly influence behavior and spatial distribution of piscivorous fishes.

Despite difficulties in parsing effects of abiotic factors on Chinook parr mortality, the predator-specific effect on Chinook mortality can be determined. Brown trout predation on Chinook parr was consistently high and likely controlled by two factors: Chinook parr growth and brown trout stocking dates. As piscivorous hatchery brown trout are gape limited by prey > 50 mm TL (e.g., Damsgård 1995), parr growth rate will influence the duration of vulnerability to brown trout predation, and therefore, may be a useful predictor for survival. My data suggested that brown trout did not consume

Chinook salmon parr after (about) May 24, when parr reached a mean length of 49 mm TL and nearly two weeks before most Chinook parr emigrated.

I observed mean daily growth rates of Chinook salmon parr that were similar to those reported from other Lake Michigan and Pacific Coast tributaries for parr captured in nursery areas. Carl (1984) observed similar mean growth rates of Chinook parr (0.28 to 1.01 mm · d⁻¹) in Baldwin and Pine Creeks, tributaries to Lake Michigan. In the Columbia River, Chinook parr growth ranged from 0.44 – 0.60 mm · d⁻¹ (Becker 1970; Dawley et al. 1986). Mean daily growth rates of Chinook salmon parr were higher in systems where parr were captured in river mouths or estuaries and at larger sizes. In the Pere Marquette and Little Manistee Rivers, also Lake Michigan tributaries, growth of Chinook salmon parr was similar to Baldwin and Pine Creeks (mean = 0.71 mm · d⁻¹) but higher than in the Muskegon River (Seelbach 1985; Zafft 1992). Growth rates of Chinook parr in the Nanaimo Estuary and Snake River were higher yet and ranged from 1.1 – 1.32 mm · d⁻¹ (Healey 1980; Connor and Burge 2003).

Growth of young Chinook is dependent on water temperature and food availability. Hence, the low growth experienced by Chinook parr in 2005 was likely caused by the lowest mean daily water temperatures of my study. If brown trout are size-selective piscivores, low parr growth rates in 2005 may have been responsible for the highest predation mortality rates I observed from 2004 – 2007. Alternatively, in 2007, the mean daily water temperature was highest for my study and predation mortality from both predators was relatively low. These conditions may have allowed for the highest rate of Chinook parr growth in all study years. The low rate of predation mortality in 2007 was likely due to predator (i.e., brown trout) abundance being much lower than in

other study years while initial Chinook parr abundance was the highest of all study years. Hence, during 2004 – 2007, Chinook parr growth rates may have been limited by water temperature and predation pressure and less influenced by density-dependent growth limitations (e.g., Chapman 1962; Mason and Chapman 1965; Unwin 1986) in the Muskegon River. This assertion is supported with the 2006 data, which indicate that intermediate water temperature and intermediate predation mortality may have resulted in intermediate growth rates of Chinook parr.

The proportion of brown trout that are piscivorous, the temporal/spatial overlap between brown trout and Chinook salmon parr, and the numbers of brown trout stocked are factors influencing survival and potential recruitment of Chinook salmon parr. Approximately 30% of all brown trout sampled in the Muskegon River were piscivorous. In 2005 and 2006, brown trout were stocked early and over multiple dates, overlapped with Chinook salmon parr for a greater duration, and inflicted greater predation mortality than in 2007. Predation mortality on Chinook by brown trout was highest in 2005, when Chinook parr growth was lowest. Although temporal overlap between brown trout and Chinook salmon parr was greatest in 2006 (~60 d vs. ~ 45 d in 2005), brown trout were stocked in early to mid April and in great numbers in 2005; 88% of all hatchery brown trout were stocked while mean Chinook TL was 39.5 mm. In 2006, only 50% of hatchery brown trout were stocked in mid April. In 2007, 60% fewer brown trout were stocked and on a later date (April 30) than in previous years, reducing the temporal overlap between brown trout and Chinook salmon parr by nearly 40%. This resulted in a 35% reduction in predation mortality by brown trout on Chinook salmon parr, indicating that timing and numbers of brown trout stocked into the Muskegon River may strongly

affect Chinook parr survival. Still, despite the considerable reduction in predation mortality on Chinook salmon parr in 2007, brown trout still consumed approximately 15% of the estimated initial parr abundance.

The migratory nature of brown trout may further affect the species interactions among important sport fishes in the Muskegon River. I compared a loss rate for brown trout representing predation and angler mortality alone (i.e., PAM approach) to a total loss rate (i.e., CPUE approach), which also incorporated losses from all sources including emigration from the upper Muskegon River. Brown trout emigration rates of 35% from the upper Muskegon River indicate that emigration may be prevalent and predation and angling mortality alone may not accurately account for total loss rates of brown trout. This is not entirely unique as higher emigration rates (50%) have been reported for brown trout in Scottish rivers (Middlemas et al. 2009).

Walleyes also may impose high predation mortality rates on Chinook salmon parr before and during Chinook out-migration from the Muskegon River though this was not observed in all study years. Unlike brown trout, walleye predation on Chinook salmon parr was inconsistent across sampling years, although this appears to have been dependent on the presence of alternate forage. Generally, Muskegon River walleyes were opportunistic predators and consumed a low biomass of small Chinook parr but a high biomass of large hatchery trout. This trend was especially obvious in May of all years when hatchery trout abundances were quite high; only 1.7% of pooled walleye diets were composed of Chinook salmon parr. In June, hatchery trout abundances were considerably lower and the proportion of pooled walleye diets composed of Chinook

increased to 9%. Hence, alternate forage fishes (i.e., hatchery trout) may buffer walleye predation mortality on Chinook salmon parr.

In Muskegon Lake, walleye did not appear to consume Chinook parr at all and prefer alternate forage species, such as alewife and gizzard shad. Nearly all Muskegon Lake walleye (70 - 100%) consumed the latter two species and the rest consumed Cyprinidae. Hatchery trout, alewife, and gizzard shad abundances were ephemeral but their availability coincided with that of out-migrating Chinook salmon parr. Thus, alternate forage appeared to buffer walleye predation mortality on Chinook parr throughout the MRES. Johnson et al. (2007) discovered a similar trend in tributaries to Lake Huron, where seasonal variability of spawning alewives buffered walleye predation on hatchery salmon smolts.

Predation mortality appeared to be highly correlated with Chinook recruitment success in the Muskegon River. Predation mortality was highest in 2005 and coincided with the lowest rate of potential recruitment. Alternatively, predation mortality was lowest and potential recruitment was highest in 2007. Total instantaneous loss (Z_{tot}) rates for Chinook salmon parr in the Muskegon River ranged from 2.5 to 2.91 during the nursery period in my study. In the Pere Marquette and Little Manistee Rivers, also Lake Michigan tributaries, total mortality rates of Chinook parr were much lower and ranged from 0 – 0.38 (Zafft 1992; Seelbach 1985) though these were hatchery-reared fish and much larger. Achord et al. (2007) reported instantaneous mortality rates of 1.38 – 2.53 for Chinook parr in a large Pacific Northwest tributary although this value was due, in part, to hydroelectric dams (Beamesderfer et al. 1990) and did not incorporate emigration as my estimate did. Instantaneous predation mortality rates (Z_{pred}) of parr, however,

appeared to be much higher in the Muskegon River (Z_{pred} range 0.22 – 0.67) as compared to rates for parr in the Columbia River (Z_{pred} range 0.09 – 0.21; Rieman et al. 1991). This result suggests that predation mortality from fishes can be very important in large Great Lakes tributaries, especially since the Muskegon River produces an order of magnitude fewer Chinook parr than west coast tributaries. Comparative data on predation mortality are lacking for other Great Lakes tributaries.

Although my methods were consistent across years, my study may have inherent bias. All sites were sampled in the same manner, however, so biases were consistent across sampling sites and years. There was no effective way to estimate Chinook parr abundance in the lower river. Therefore, I could not quantify population consumption by walleyes of Chinook salmon parr in the lower Muskegon River, which means my predation mortality estimates were likely conservative. Movement of fishes from my study sites would be interpreted as mortality (combined with natural mortality), thereby underestimating survival (especially of Chinook parr). Additionally, I used stocking values of trout as initial abundances and assumed no natural reproduction of hatchery brown and rainbow trout; abundance estimates for brown and rainbow trout may also be conservative. Regardless, my estimates of predation mortality on Chinook salmon parr provide a baseline to which future studies can be compared.

Management Implications

Trophic interactions among walleyes, stocked rainbow and brown trout, Chinook salmon parr and forage fishes have large implications for effective management of these species in the Muskegon River (Figure 2.9). The timing, location and strength of these interactions may determine the efficacy of fishery management in promoting future

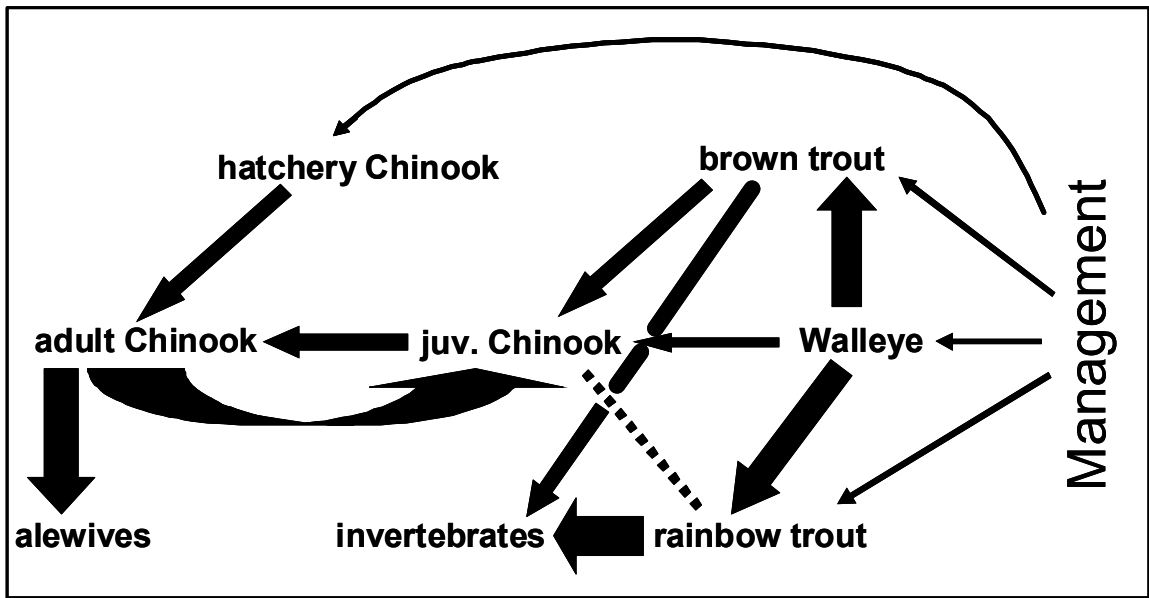


Figure 2.9. Conceptual food web showing potential interactions between important sport fishes and their prey in the Muskegon River. Arrows point to the affected species and arrow thickness represents the intensity of the interaction. The dashed line represents an indirect interaction between rainbow trout and Chinook salmon parr. All interactions are controlled by management actions such as stocking.

productivity of valuable sport fisheries in the MRES. Fishery managers can control predation mortality on Chinook salmon parr through stocking and harvest regulations of piscivores (e.g., Krueger and Hrabik 2005; Harvey and Kareiva 2005).

Predation mortality on juvenile stages may have a greater impact on wild salmon recruitment variability in freshwater versus marine habitats (Myers 2001) though this may be seasonally dependent. I estimated predation mortality rates on Chinook parr that ranged from 18% to 49% during the nursery period (April – June) in the Muskegon River. Rieman et al. (1991) estimated a predation mortality rate on juvenile Chinook of approximately 30% for the same time interval in a Columbia River reservoir though predation may increase substantially by August when temperatures are much higher. Chinook salmon smolts out-migrate from the Muskegon River long before August, making their nursery residence much shorter than in west coast tributaries. Tributary systems in both regions contain important top predators that are major sources of variable mortality for out-migrating Chinook salmon. In Lake Michigan tributaries, walleye and brown trout are the main predators of Chinook salmon parr while the northern pikeminnow (*Ptychocheilus oregonensis*) is the dominant predator in the Pacific Northwest (Beamesderfer et al. 1990; Friesen and Ward 1999) as it accounts for most (78%) of the predation mortality on juvenile salmonids in some tributaries (Rieman and Beamesderfer 1990; Rieman et al. 1991).

Manipulation of predator abundance may be helpful in assessing its relative contribution to overall ecosystem structure and function (e.g., Paine 1966; Navarrete and Menge 1996; Rand and Stewart 1998). Management actions to remove northern pikeminnow have resulted in considerable reduction in salmon smolt mortality (Rieman

and Beamesderfer 1990; Rieman et al. 1991). Removal of northern pikeminnow is dependent on angler participation and a sustained exploitation rate. In the Muskegon River, however, removal of piscivorous hatchery trout can be accomplished by simply curtailing stocking practices or creating effective stocking windows, thereby substantially reducing parr mortality. Unlike in Pacific Northwest tributaries, where hydropower dams are the major determinants of salmon parr mortality, predation appears to be a significant source of Chinook salmon parr mortality in the Muskegon River. When brown trout abundances were significantly reduced (i.e., 2007), survival of Chinook salmon parr increased substantially and potential recruitment nearly tripled compared to 2005, when predation mortality peaked. Stocking of Chinook salmon parr into tributaries can also be timed to ensure proper size and imprinting have been achieved and that alternate prey are available. Johnson et al. (2007) found the aforementioned factors contributed strongly to increased survival rates of stocked Chinook salmon parr in Lake Huron.

While fishery managers must direct stocking efforts to maximize hatchery efficiency and Chinook salmon parr survival, they must also supplement other valuable sport fish stocks. Although walleye are not a highly prized sport fish in the Muskegon River (proper), angler effort and harvest are high for walleye in Muskegon Lake and near-shore Lake Michigan (Hanchin et al. 2007). On the other hand, creel records indicate that fishing effort and harvest rates for brown trout are extremely low in all MRES habitats. Further, my empirical observations suggest that brown trout are the most significant source of variability in wild Chinook salmon recruitment. Therefore, to improve recruitment of Chinook salmon smolts to the Lake Michigan fishery, brown

trout stocking should be altogether eliminated in rivers that produce wild Chinook salmon parr.

Natural recruitment of Pacific salmonids in the Great Lakes has become an extremely important source of adult salmon in the past few decades. The increasing numbers of wild-produced salmon have led to very high adult abundances such that they cannot be supported by the forage base. Effective management of the Lake Michigan Chinook salmon fishery depends on reliable estimates of adult salmon harvest, adult spawner returns and Chinook salmon parr production in important tributaries. Fishery managers no longer have direct control over riverine Chinook salmon production which makes annual assessments of wild Chinook recruitment increasingly critical towards effective fishery management in Lake Michigan tributaries. My study provides a template for estimating wild Chinook recruitment although more detailed analyses may provides further insight into long-term Chinook salmon management. Detailed analysis of piscivore feeding behavior (i.e., functional response) in important tributaries may further elucidate predator diet trends such as those I have described. Such work could inform modeling studies that attempt to investigate complex spatial interactions involved in Chinook salmon migration (Petersen and DeAngelis 2000) and would allow for the evaluation of combined effects of environmental variability and predation on Chinook parr survival. Integrating piscivore feeding behavior, Chinook salmon habitat selection and migratory behavior (e.g., Jager et al. 1997, Railsback and Harvey 2002), and fluctuating abiotic variables in such a modeling approach may improve mechanistic understanding of the recruitment process of Chinook salmon in the Great Lakes.

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Chapter III

Feeding Behavior of Walleye and Brown Trout and its Influence on Chinook Salmon Recruitment in a Lake Michigan Tributary

Abstract

A major factor regulating variability in Chinook salmon (*Oncorhynchus tshawytscha*) recruitment is predation on early life history stages. Predation rate is determined by a number of factors including availability of alternative prey to predators. To better understand the role of alternative prey on predator diet selection and Chinook parr mortality and potential recruitment from 2004 to 2007, I determined prey densities and sizes, predator diet composition, feeding behavior (size- and species-specific prey selection), and functional response relationships for walleyes (*Sander vitreus*) and brown trout (*Salmo trutta*) in the Muskegon River, a tributary of Lake Michigan. Walleye diets were largely composed of brown trout and rainbow trout (*O. mykiss*) in all study years (80% - 95% by weight). Walleyes were size-selective for smaller brown and rainbow trout than were available in the environment but walleye prey size was independent of predator size. In general, walleyes showed neutral selection for all prey species but in some years showed positive selection for rainbow trout and negative selection for Chinook parr. I fit a Type-II curve to describe the functional response by walleyes to varying abundances of prey. Hatchery brown trout diets were largely composed of

Chinook salmon parr in April and May (30% - 68% by weight) and invertebrates (100% by weight) in June. Brown trout selected for parr that were smaller than the average parr length in the environment, although prey size was independent of predator size. Chinook parr were positively selected for by brown trout only in April. I fit a Type-I curve to describe the functional response by brown trout to variable abundances of Chinook salmon parr. The presence of alternate prey significantly influenced walleye predation on Chinook salmon parr while brown trout appeared to be limited by size of Chinook parr. Functional response relationships suggested that predator management scenarios employing removal of brown trout would have the greatest positive impact on Chinook salmon recruitment. Management efforts to reduce brown trout abundance via stocking could decrease predation mortality of Chinook salmon parr by up to 23.4% thereby improving potential recruitment.

Introduction

In the Pacific Northwest and the Laurentian Great Lakes, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (parr) survival, and thus recruitment, can vary annually due to environmental factors such as temperature and flow, and biotic factors such as predation and competition (Beamsderfer et al. 1990; Bradford 1994; Jager et al. 1997; Einum et al. 2008). In the Pacific Northwest, predation is thought to be the primary driver regulating survival (Peterman and Gatto 1978; Fresh et al. 2003; Chapter 2). In U.S. tributaries to the Pacific Ocean, the northern pikeminnow (*Ptychocheilus oregonensis*), smallmouth bass (*Micropterus dolomieu*) and Caspian tern (*Hydroprogne caspia*) are responsible for the majority of predation mortality experienced by Chinook salmon parr and smolts (Tabor et al. 1993; Roby et al. 2003; Antolos et al. 2005). Piscivore feeding behavior in the Great Lakes, on the other hand, has been little studied with respect to its potential impact on survival of Chinook salmon parr (see Johnson et al. 2007).

In the Muskegon River, a tributary to Lake Michigan, survival of Chinook salmon parr is influenced by walleye (*Sander vitreus*) and brown trout (*Salmo trutta*) predation (Chapter 2). Brown trout, despite their smaller size (mean length = 164 mm), consume more Chinook salmon parr as a group than the much larger walleye. Fritts and Pearsons (2006) found a similar trend in the Yakima River, Washington, where smaller predators consumed more salmon parr as a group than larger predators. However, the presence of alternate prey may buffer predation rates on Chinook salmon parr, thereby reducing overall predation mortality rates (e.g., Forney 1974). My objectives were to 1) describe the feeding behavior of walleye and brown trout as a function of variable abundances and

sizes of primary and alternate forage, 2) determine prey preference and size selection of piscivorous walleye and brown trout, and 3) develop predator functional response relationships to evaluate management scenarios for their impact on potential Chinook salmon recruitment. Since predators generally select prey based on prey size (Bannon and Ringler 1985; Juanes 1994), I hypothesized that predation mortality on Chinook salmon parr will be size selective and will vary with availability of alternate prey. I further hypothesized that alternate prey can buffer size-structured predation mortality of Chinook salmon parr in the Muskegon River (e.g., Czesny et al. 2001). If the abundance of alternate prey decreases, predation mortality on Chinook parr should subsequently increase.

Study Site

The Muskegon River extends 365 km from Houghton Lake in north-central Michigan to Muskegon, Michigan, where it empties into Lake Michigan (Figure 3.1). I focused my efforts on the (ca.) 22.5 km salmonid nursery section of the Muskegon River between Croton and Newaygo (see Godby et al. 2007). This section of river experiences mean discharge rates of approximately $84.9 \text{ m}^3 \cdot \text{s}^{-1}$ (range $60.9 - 260.8 \text{ m}^3 \cdot \text{s}^{-1}$) from April to June and the substrate is predominantly cobble and gravel, which provides excellent spawning habitat for Chinook salmon and other important sport fishes such as walleye and steelhead (*O. mykiss*) (Auer and Auer 1990; Merz et al. 2004; Quinn 2005).

Methods

Fish Abundance and Size

Abundance and size of Chinook salmon parr and Cyprinidae were estimated in the Muskegon River from 2004 - 2007. In 2004, I used a 2.4 m diameter auger-style smolt trap to capture out-migrating Chinook salmon parr from May 6 to June 29. Fish were

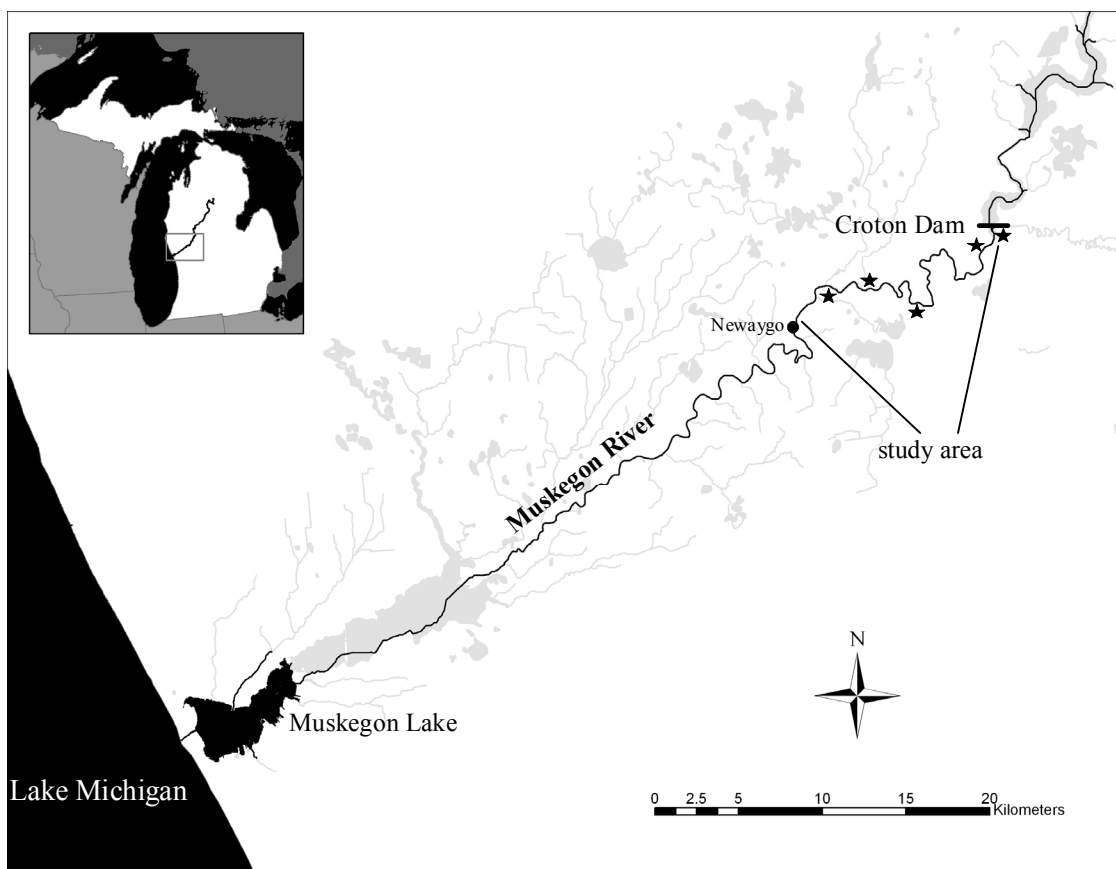


Figure 3.1. The location of the Muskegon River and Muskegon Lake, Michigan. Stars indicate barge electrofishing reference sites (see Carl 1980) used to estimate population abundance of Chinook salmon parr.

identified, counted, weighed (nearest 0.1 g) and measured (TL mm) each day. Densities of Chinook salmon parr and cyprinids were estimated for the remaining years (April 19 – June 15, 2005; April 20 – June 7, 2006; May 8 – June 6, 2007) using a barge-style electrofishing unit (3 Amps, 240 V) along daytime 100 m transects, run upstream, at five established reference sites (Carl 1980) (Figure 3.1). I used a pass depletion protocol (e.g., Zippin 1956, 1958) because Chinook parr were generally too small (< 50 mm) for effective mark and recapture estimates. I sampled each reference site twice a month and sampled most sites 5 times in a given field season. I weighed and measured a sub-sample of 30 Chinook salmon parr from each electrofishing transect and counted and batch weighed the remaining individuals. Abundances of Chinook parr and Cyprinidae were estimated for the whole river by multiplying the mean density (# m⁻¹) of fish at the five reference sites on each sampling date by the total nursery shoreline (22.5 km x 2 sides = 45 km).

I estimated the initial abundance of Chinook salmon fry at swim-up by developing a linear relationship between parr length and abundance over time. I assumed swim-up occurred at 37 mm TL (length at emergence, Beachum and Murray 1990). In addition, I tested for differences in mean length (TL, mm) of Chinook salmon parr across years using a general linear model (GLM). Length was the dependent variable while water temperature was the covariate, and sampling date and year were included as independent variables. Length data for 2004 were not included as capture methods and locations differed between 2004 and 2005 – 2007.

Walleyes, brown trout, and rainbow trout were collected using a barge electrofisher using the aforementioned methods and reference stations in addition to

collections with a 20' Smith Root boom-style AC electrofishing boat (3 Amps, 240 V). Boom-electrofishing transects were run in a downstream fashion and were always performed during the day. Upon capture, fish were placed in a 189-liter recirculating live well and counted at the end of each transect. Population abundances of these three species were estimated using data from boom electrofishing transects. Date-specific abundances of brown trout and rainbow trout were estimated by scaling catch per unit effort (CPUE, # hr⁻¹) in electrofishing transects to the number of trout stocked. The decline in CPUE and abundance of stocked hatchery trout was assumed to result from harvest, predation and emigration from the river. I used linear interpolation to determine fish abundances for dates in between sampling efforts. Walleye abundance was calculated in the same way, but initial abundances were based on estimates of spawning walleye abundance in the Muskegon River (approximately 38,000 individuals) in 2002 (Hanchin et al. 2007).

Predator Diet Composition

The methods used to determine predator diet composition are reported in detail in Chapter 2. Here, I provided an abbreviated version. At the completion of each electrofishing transect, predators were measured (TL, mm), weighed (0.01kg) and stomach contents flushed from live fish using a garden sprayer (e.g., Seaburg 1957); whole stomachs were excised from deceased fish and live fish were released. Diet items were qualitatively identified (when possible) in the field and then preserved in 95% ethanol or 10% formalin. In the laboratory, undigested stomach contents were measured (TL mm), weighed (nearest 0.1mg wet weight) and identified. Fish prey items were identified to species when possible, while invertebrate prey items were identified to

order. Partially digested prey fish were identified based on diagnostic structures and compared to weight-at-length data of forage fish from the Muskegon River (Chapter 2). I used the “meal-turnover” method described by Vigg et al. (1991) to quantify the daily rations of walleye and brown trout in the Muskegon River (see Chapter 2).

Predator Feeding Behavior

I evaluated predator feeding behavior by determining if predators were selecting prey by size or species. Size-selective predation was determined by comparing mean length of ingested prey to mean prey length in the environment (e.g., Wankowski 1979; Shively et al. 1996). I calculated monthly mean residuals for length (mean length_{ingested} – mean length_{environment}) of each prey type. Piscivores were considered size-selective if the mean length of ingested prey was significantly greater or less than the environmental mean (based on 95% confidence intervals). In addition, I calculated the ratio of prey length to piscivore length to determine whether prey size consumed was correlated with piscivore size. I estimated a maximum prey/predator ratio (as % of TL) for piscivorous walleye and brown trout, which was based on the largest prey/predator ratio observed for each predator species. To determine if predators selected prey species I used Chesson’s α (Chesson 1983):

$$\alpha_i = \frac{r_i/n_i}{\sum_{i=1}^m r_i/n_i} \quad i = 1, \dots, m \quad (1)$$

where r_i and n_i are the number of prey species i in a predator’s diet and the environment respectively, and m is the number of prey types. Alpha values were calculated for individual piscivores and averaged for April, May and June of each study year. Alpha values $> 1/m$ indicate that a predator consumed a prey species in greater proportion than

prey abundance would suggest and hence, the predator was foraging in a species-selective manner. I used Chesson's index because α does not change with food density unless consumer behavior changes. Hence, it is appropriate for detecting behavior such as "switching" (Murdoch 1969). I assumed a constant biomass of invertebrates ($9.9 \text{ kg} \cdot \text{ha}^{-1}$) as data were scarce for my study years (C. Riseng, University of Michigan unpublished data). Rainbow trout were predominantly insectivorous and did not feed on Chinook salmon parr, thus were not considered in this analysis.

Predator Functional Response

I parameterized a multi-species functional response model (Abrams 1987) to quantify predator feeding rates in the presence of preferred and alternate prey. To do this I estimated piscivore consumption ($\text{g} \cdot \text{day}^{-1}$) from prey abundance ($\text{g} \cdot \text{ha}^{-1}$) and fitted a Type-II functional response curve using TableCurve 2D© v 5.01 (SYSTAT software Inc.). This curve predicts the amount of each prey type an average walleye will consume daily (N_e , g/day):

$$\begin{aligned}
 N_{e,1} &= \frac{a_1 N_1}{1 + a_1 T_{h,1} N_1 + a_2 T_{h,2} N_2 + a_3 T_{h,3} N_3 + a_4 T_{h,4} N_4} \\
 N_{e,2} &= \frac{a_2 N_2}{1 + a_1 T_{h,1} N_1 + a_2 T_{h,2} N_2 + a_3 T_{h,3} N_3 + a_4 T_{h,4} N_4} \\
 N_{e,3} &= \frac{a_3 N_3}{1 + a_1 T_{h,1} N_1 + a_2 T_{h,2} N_2 + a_3 T_{h,3} N_3 + a_4 T_{h,4} N_4} \\
 N_{e,4} &= \frac{a_4 N_4}{1 + a_1 T_{h,1} N_1 + a_2 T_{h,2} N_2 + a_3 T_{h,3} N_3 + a_4 T_{h,4} N_4}
 \end{aligned} \tag{2}$$

where $N_{e,i}$ is the biomass of prey i consumed ($\text{g} \cdot \text{day}^{-1}$), a_i is the rate constant for capturing prey while searching, $T_{h,i}$ is the handling time (hours) associated with species i , N_i is the abundance of prey species i ($\text{g} \cdot \text{ha}^{-1}$) and subscripts represent the prey type (1- Chinook parr; 2- Cyprinidae; 3- brown trout; 4- rainbow trout). The shape of the

functional response curve was established by minimizing the geometric mean of the sums of squares for all species and simultaneously solving for a_i and $T_{h,i}$. For brown trout, I fitted a Type-I functional response to variable abundance of Chinook salmon parr.

Using my estimated functional response for walleyes, I evaluated the potential outcome of predator-prey interactions that may result from various management manipulations. I accomplished this by removing individual prey and/or predator types, then simulated the feeding behavior of walleyes in response to each manipulation and compared the results to my previous empirical analysis (Chapter 2). Since my foraging model was empirically derived, an inherent assumption was that predator size/species selectivity would not change in response to manipulations. I used a 4 x 4 x 4 factorial experimental design to simulate removals (0%, 25%, 50%, 100%) of walleyes, brown trout and rainbow trout to determine the effect on survival of Chinook salmon parr and hence, Chinook salmon recruitment. Results from simulated removals were compared to a baseline value, which was defined as the mean survival rate of Chinook parr observed during the study ($S = 0.51$; Chapter 2). Although the effects of walleye removal from the Muskegon River would take several years to detect since individuals are long-lived (up to 18 years), I assumed a rapid change in population abundance.

Results

Fish Abundance and Size

Peak abundance of Chinook salmon at the swim-up (fry) stage averaged 491,504 (\pm 27,864) parr across all sampling years and ranged from 459,717 to 511,712 (Table 3.1, Figure 3.2). The swim-up stage was observed between April 10 and April 20 in all years. After swim-up, Chinook salmon parr abundance decreased by approximately 7,282 parr .

Table 3.1. Regression statistics to estimate peak abundance of Chinook salmon at the swim-up (fry) stage.

Year	n	r²	F statistic	p-value	Slope	Intercept	Peak abundance
2004	na	na	na	na	na	na	491,504*
2005	5,503	0.82	8.951	0.096	-22,258	1,283,263	459,717
2006	6,984	0.91	19.313	0.048	-22,409	1,332,217	503,084
2007	5,170	0.74	8.703	0.06	-20,032	1,252,896	511,712

*mean value from 2005 – 2007 was used.

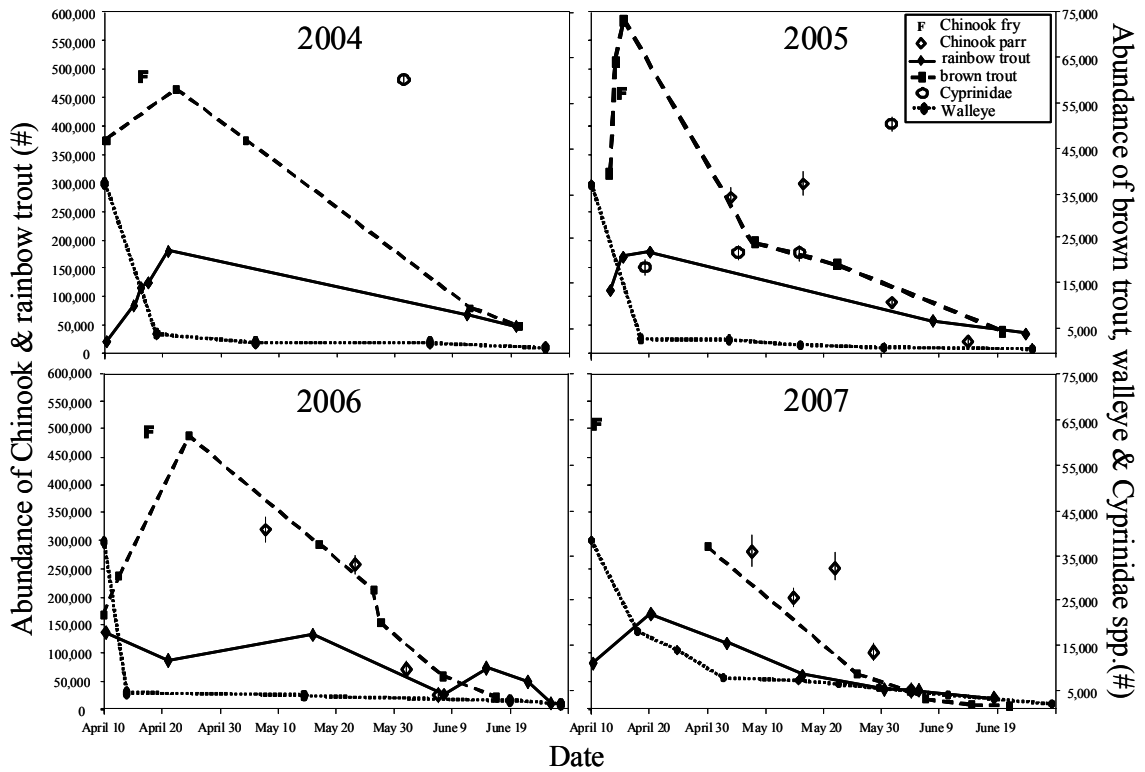


Figure 3.2. Intra- and inter-annual variation in population abundances of Chinook salmon fry (“F”) at swim-up and parr (open diamonds; mean \pm 95% confidence intervals), Cyprinidae (open circles; mean \pm 95% confidence intervals), brown trout, rainbow trout and walleye. The 2004 abundance estimate for Chinook salmon fry is the mean of Chinook salmon fry production from 2005 to 2007. Abundance of Cyprinidae was not available for 2006 or 2007.

day⁻¹ (range 6,695 to 7,766) throughout the spring (Figure 3.2, Chapter 2). Chinook parr size (TL, mm) did not differ significantly across years ($F_{2,15} = 1.584$, p-value = 0.238), although sampling date ($F_{1,15} = 19.789$, p-value < 0.0001) and water temperature ($F_{1,15} = 28.293$, p-value < 0.0001) were significant sources of inter-annual variation in parr length (Figure 3.3).

Abundance of trout, walleyes and Cyprinidae were fairly consistent across years. Annual numbers of hatchery trout stocked from 2004 – 2007 averaged 259,661 individuals. There was no relationship between trout total length and stocking date. Rainbow trout stocking levels were consistent in all study years ($189,000 \pm 11,483$; mean TL = $174 \text{ mm} \pm 3.7$) but brown trout (mean TL = $164 \text{ mm} \pm 3.2$) stocking dropped by approximately 40% from nearly 85,000 in 2004 – 2006 to approximately 35,000 individuals in 2007 (Figure 3.2). In all years, brown trout abundance declined rapidly following stocking events and by mid June, brown trout were rare (Figure 3.2). This decreasing trend was less pronounced for rainbow trout, which appeared relatively abundant throughout the sampling season (Figure 3.2). Most walleyes ($314 \text{ mm} \leq \text{TL} \leq 810 \text{ mm}$) departed the Muskegon River immediately post-spawn (approximately April 1) but an estimated 2,000 to 3,000 adult walleyes (mean abundance = 1,968, range: 987 – 4,641) remained through June in all years (Figure 3.2). Abundance of Cyprinidae generally increased throughout the sampling season (2005) (Figure 3.2) and their mean length was $55.5 \text{ mm} \pm 1.8$.

Predator Diet Composition

I collected and analyzed diets from 707 walleyes in the upper Muskegon River (62 in 2004, 366 in 2005, 66 in 2006, 213 in 2007). For all years, approximately 55% (range:

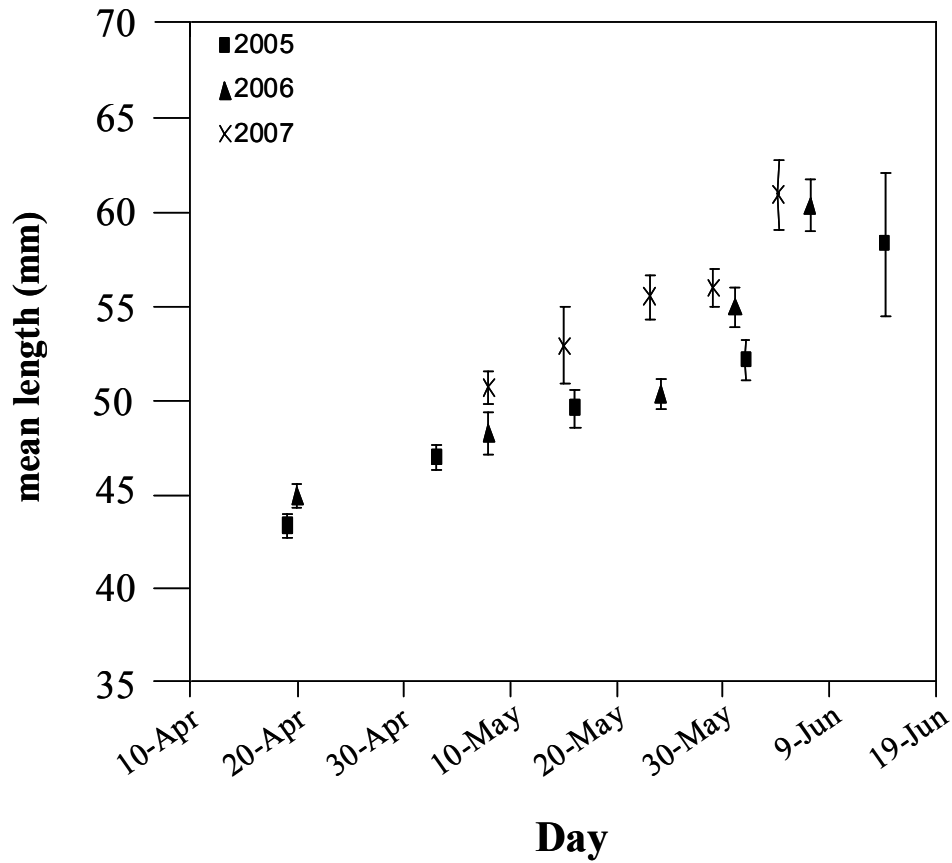


Figure 3.3. Mean length (mm TL) of Chinook salmon parr collected from 5 reference sites throughout the spring (April – June) of each study year. Mean length did not differ significantly among sampling years (2005 – 2007). All error bars represent 95% confidence intervals. Length data for 2004 were not included due to differences in capture method and location.

37% – 74%) of the walleyes examined had empty stomachs, but most of those walleyes (177) were captured immediately post-spawn in 2005 (early April). Otherwise, walleyes with stomach contents were 98.3% piscivorous and consumed large proportions of hatchery brown and rainbow trout. From 2004 to 2007, 74% of walleyes with prey in stomachs consumed hatchery trout whereas only 12% of walleyes consumed Chinook salmon parr. Rainbow trout and brown trout made up from 80 to 95% of walleye diet (by weight) in all months across all study years (Figure 3.4). The proportion of diets composed of Chinook salmon parr was much smaller and ranged from 0.1 to 15% of total diet biomass. Walleyes also consumed Cyprinidae in greater proportion in June when hatchery trout and Chinook salmon parr abundances were low.

I collected and analyzed diets from 268 brown trout from 2005 to 2007. Approximately 70% (range: 54 – 91%) of all brown trout sampled contained diet items and of those, 30% (range: 26 – 38%) consumed Chinook salmon parr. In April, the proportion of Chinook parr in brown trout diets was relatively high (44% by weight) but declined in May (29% by weight, range: 25 – 38%). In June, brown trout diets were composed entirely of macroinvertebrates (*Trichoptera* and *Ephemeroptera* spp.) (Figure 3.5).

Predator Feeding Behavior

The maximum prey/predator ratio for Muskegon River walleye was 47% TL. Most prey fell well under this maximum. The lengths of brown trout and rainbow trout consumed by walleyes averaged 30% of walleye lengths, Cyprinidae lengths averaged 22% and Chinook salmon parr only averaged 10% of walleye lengths (Figure 3.6). However, none

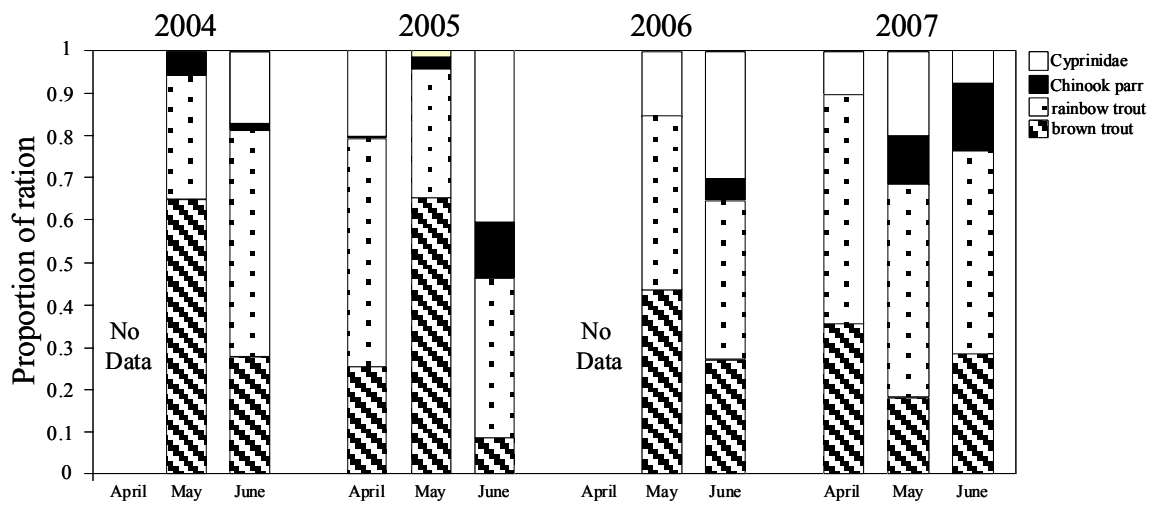


Figure 3.4. Proportions of mean daily ration ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) of Muskegon River walleye within and among study years. Cyprinidae were almost entirely composed of common shiners (*Notropis cornutus*) and bluntnose minnows (*Pimephales notatus*).

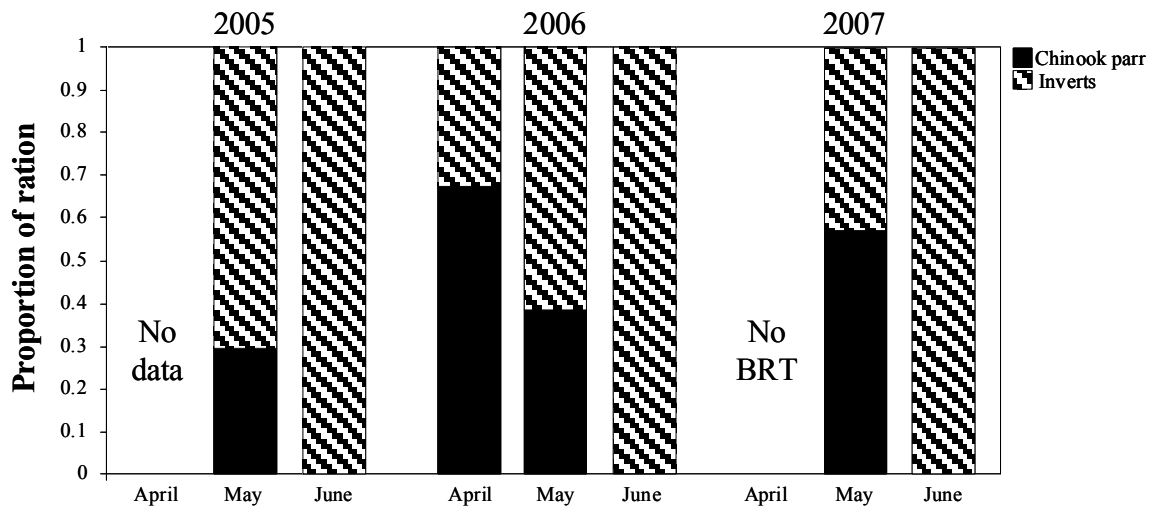


Figure 3.5. Proportions of mean daily ration (g · g⁻¹ · day⁻¹) of Muskegon River brown trout (“BRT”) within and among study years. Diet data were not available for April of 2005 and brown trout were not stocked in April of 2007.

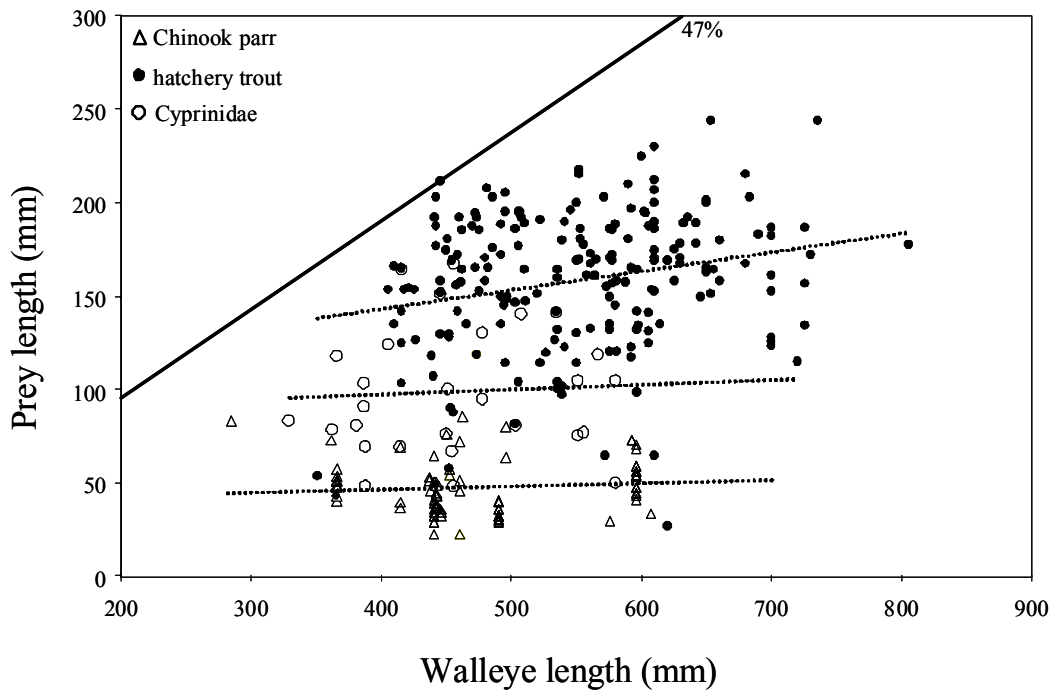


Figure 3.6. Individual walleye total length is plotted against individual prey total length. The solid line indicates the maximum prey/predator ratio (47% TL) observed for Muskegon River walleyes. The dashed lines represent the slopes of prey/predator lengths for each prey type; the mean prey/predator length ratio for hatchery brown trout and rainbow trout (upper) was 30% of walleye length, Cyprinidae (middle) were 22% and Chinook salmon parr (lower) were only 10% of walleye TL. None of the species-specific regressions has a slope significantly different from zero.

of the aforementioned prey/predator relationships were statistically significant, indicating that relative prey size was independent of walleye size. Walleyes were size-selective predators for individual hatchery rainbow trout and brown trout as ingested prey sizes were generally smaller than the mean prey size available in the environment (Figure 3.7).

Walleyes exhibited neutral selection for individual prey types as a general trend although they did strongly select for rainbow trout in 2005 and 2007. Conversely, walleyes selected against Chinook salmon parr in 2004 (June), 2006 and 2007 (Figure 3.8).

Brown trout consumed Chinook prey that averaged 21% of their total length and nearly all prey fish were much smaller than the estimated maximum prey-predator length ratio of 30% (Figure 3.9). The mean size of Chinook salmon parr ingested by brown trout was significantly smaller than the mean size of parr in the environment (Figure 3.10).

Brown trout also exhibited species-selective feeding behavior and strongly selected for Chinook salmon parr in April (2006), were neutral towards parr in May and selected against parr in June (Figure 3.11). The trend in prey selection was reversed for invertebrates; brown trout selected against invertebrates in April (2006), were neutral towards them in May and exclusively selected invertebrates in June (Figure 3.11).

Predator Functional Response

The functional response of walleyes to variable abundance of Chinook salmon parr appeared to plateau at approximately $1.25 \text{ g} \cdot \text{day}^{-1}$. The walleyes' functional response to Cyprinidae appeared to approach an asymptote but did not plateau at the abundances observed. Much higher levels of brown trout and rainbow trout were required to satiate

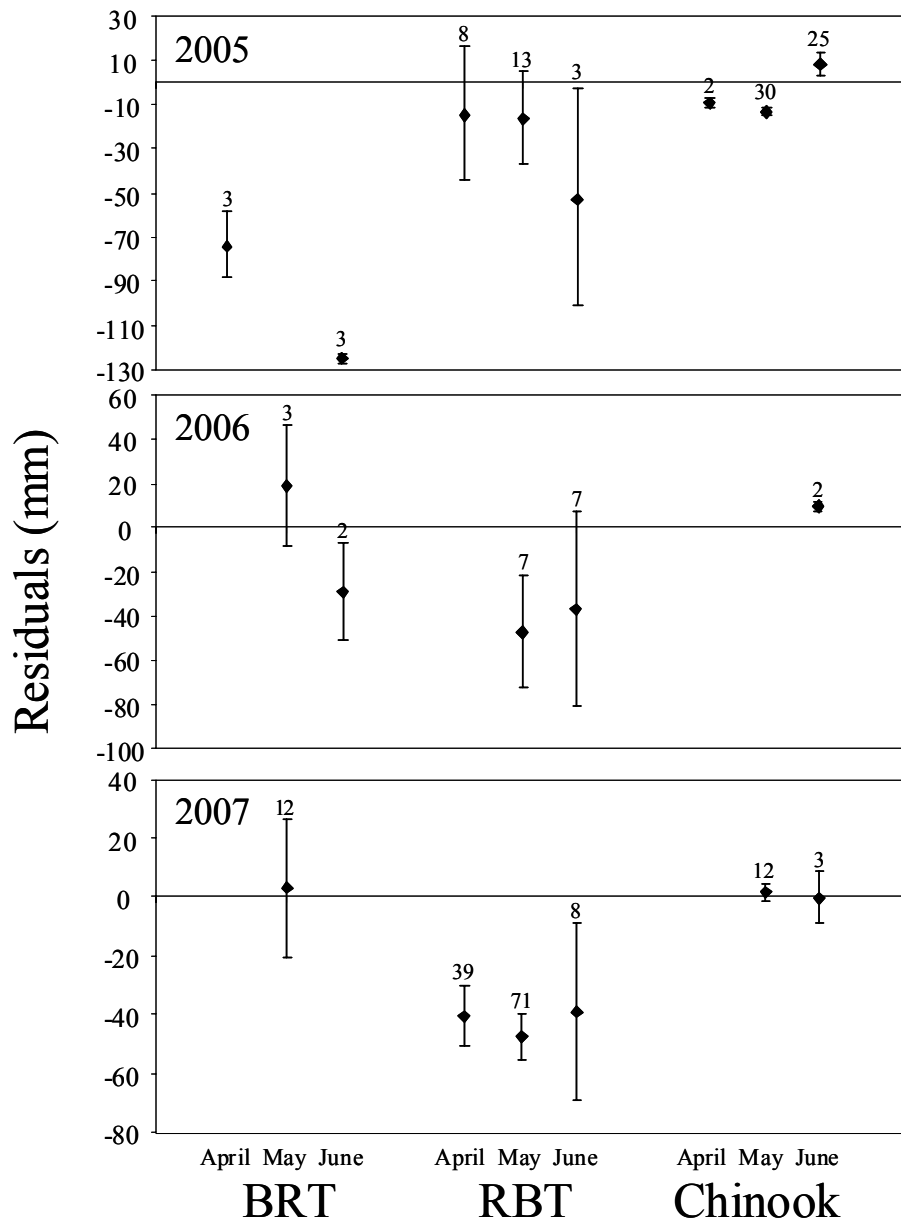


Figure 3.7. Size of prey fish species consumed by walleyes was compared to mean size of prey fish species in the environment in 2005 – 2007 using mean residuals. “BRT” represents brown trout and “RBT” represents rainbow trout. Error bars represent 95% confidence intervals and sample sizes are listed above error bars. Data on lengths of walleye prey were unavailable for 2004.

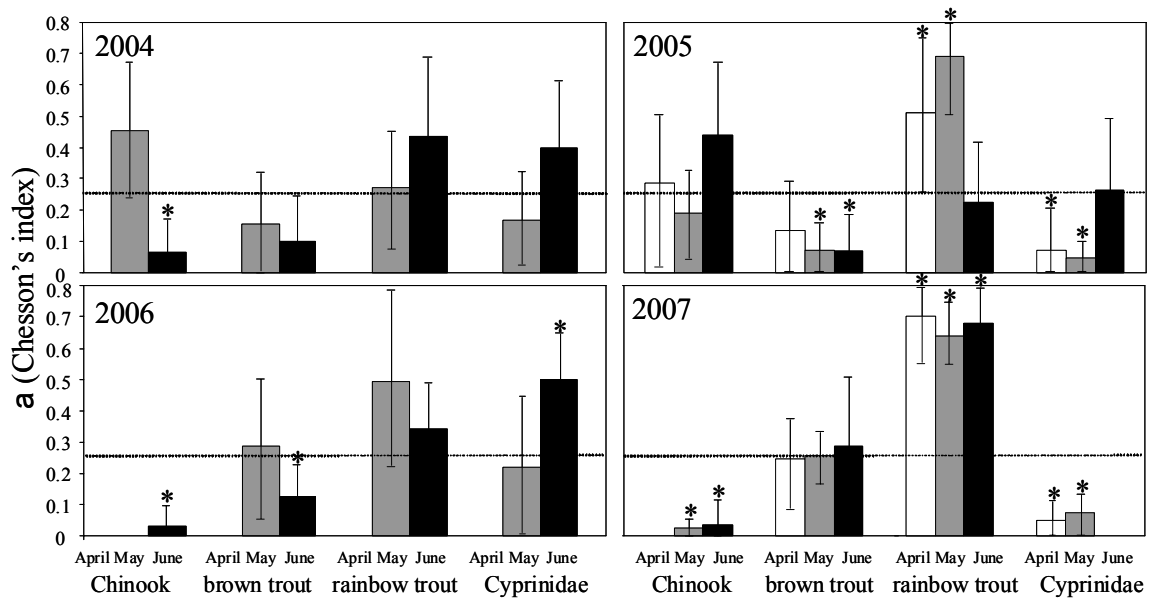


Figure 3.8. Chesson's index of prey selection for Muskegon River walleyes from 2004 – 2007. Error bars represent 95% confidence intervals and the dotted horizontal line in each box represents neutral selection for individual prey. Asterisks represent prey for which walleye show positive or negative selection.

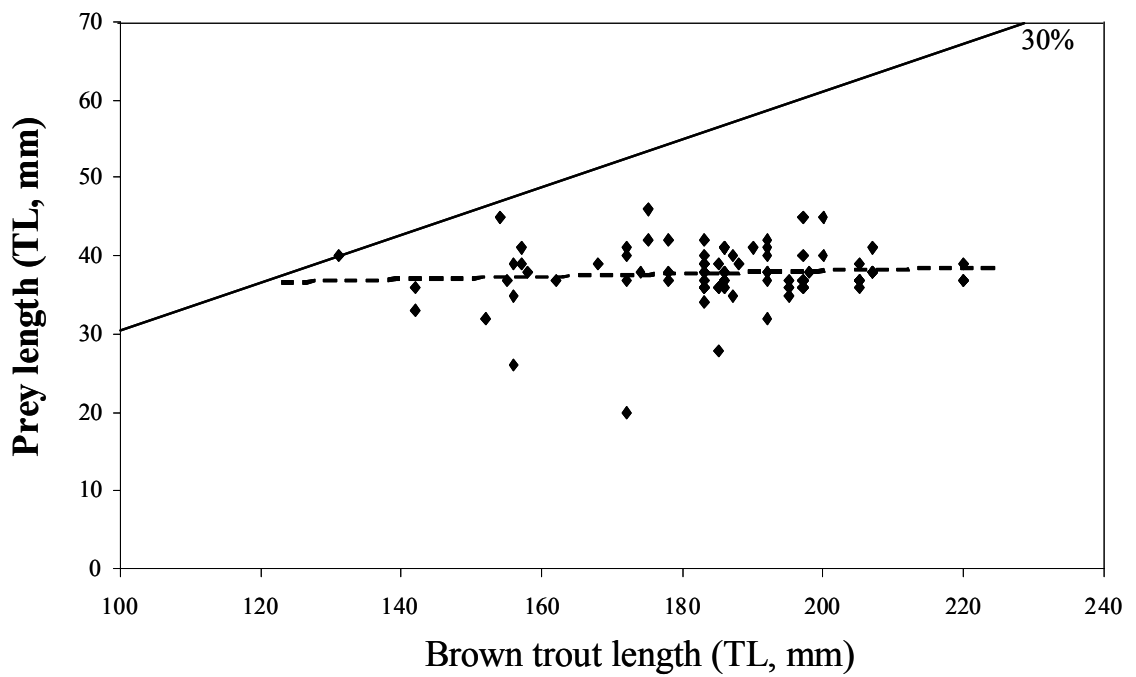


Figure 3.9. Length of individual brown trout is plotted against length of Chinook prey. The solid line indicates the maximum prey/predator ratio (30% TL) observed for brown trout in the Muskegon River. The dashed line represents mean Chinook salmon prey size, which was on average ~21% of predator length. The slope of this regression is not significantly different from zero. Data on lengths of brown trout prey were not available for 2004 or 2005.

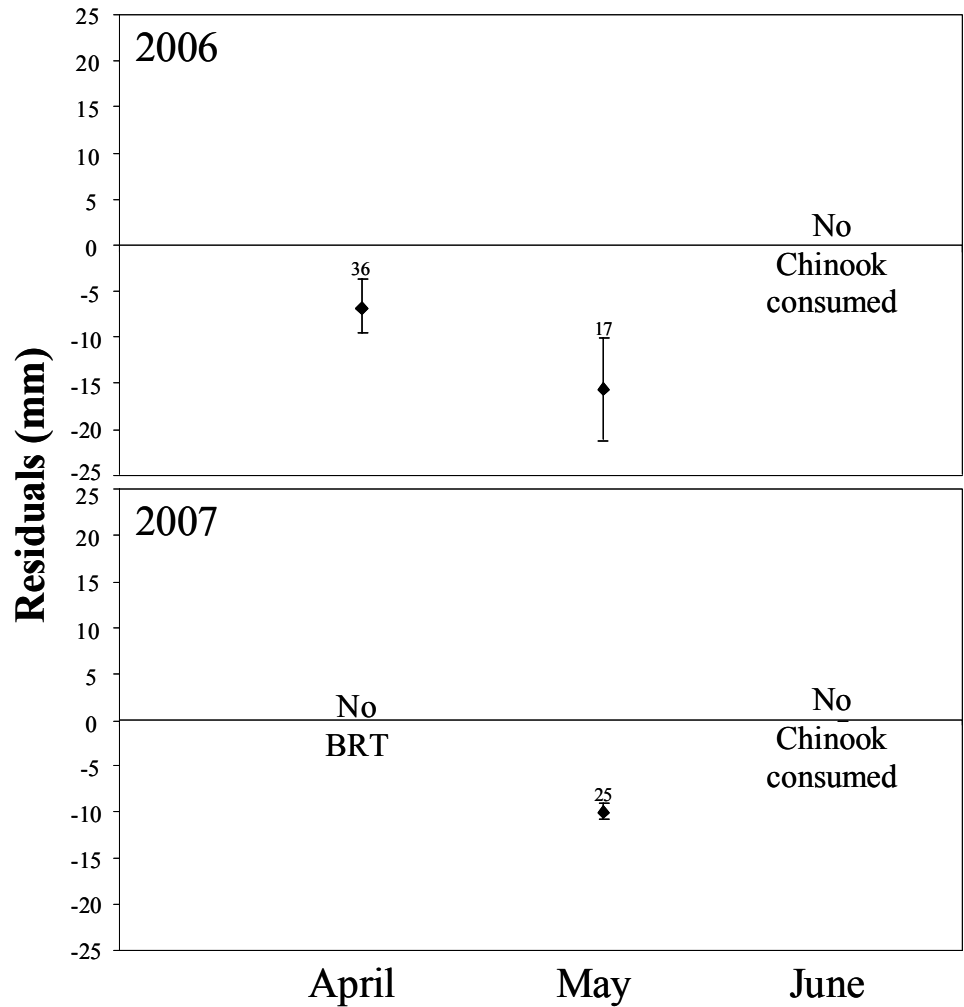


Figure 3.10. Size of Chinook salmon parr consumed by brown trout (“BRT”) compared to mean size of Chinook parr in the environment in 2006 and 2007 using mean residuals. The horizontal line at “0” represents the mean standardized prey size in the environment. Error bars represent 95% confidence intervals and sample sizes are listed above error bars. Diet data of brown trout were unavailable for 2004 and were insufficient for analysis in 2005. Brown trout were not stocked in April of 2007.

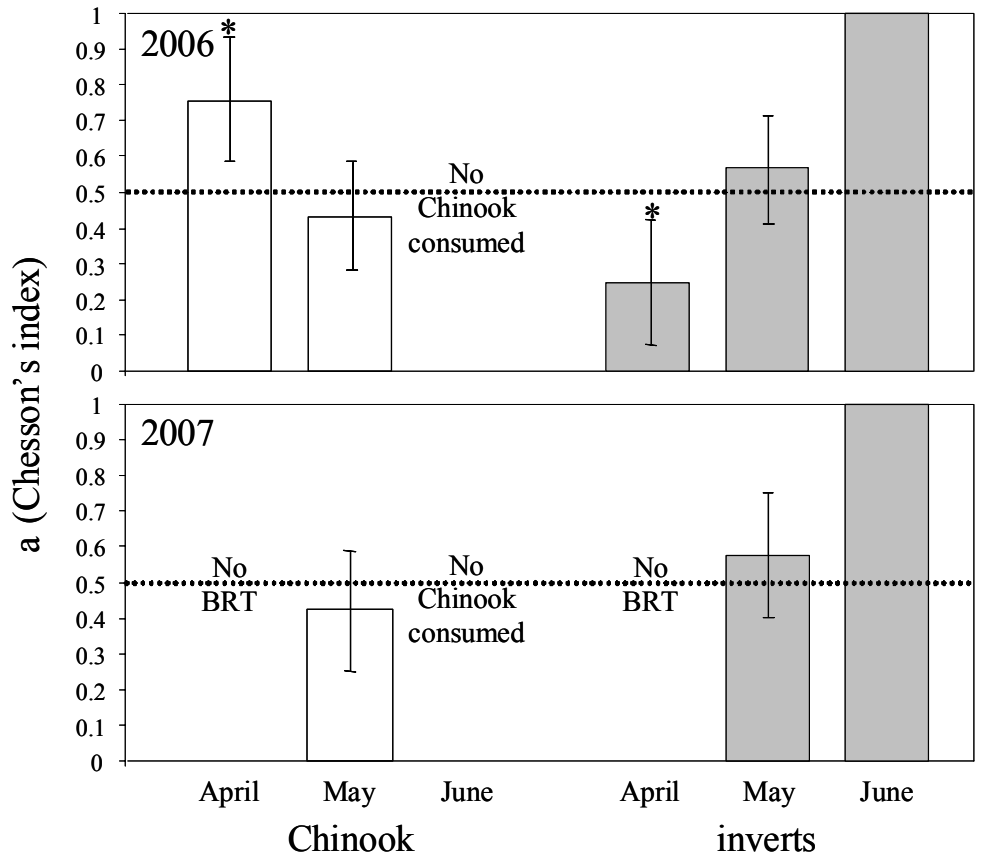


Figure 3.11. Chesson's index of prey selection for brown trout caught in the Muskegon River in 2006 and 2007. Error bars represent 95% confidence intervals; the dotted horizontal line in each box represents neutral selection. The asterisks represent positive and negative selection for individual prey types (Chinook salmon parr, macroinvertebrates).

walleye (Figure 3.12). Walleyes showed the greatest predatory response ($a_i = 145$) to increasing rainbow trout abundance, a very low response to Cyprinidae ($a_i = 1.37$) and Chinook parr ($a_i = 0.49$) and the lowest response to brown trout ($a_i = 0.03$) (e.g., Pervez and Omkar 2005) (Table 3.2). Handling times were lowest for brown and rainbow trout ($T_h = 0.17$), higher for Chinook parr ($T_h = 0.43$) and highest for Cyprinidae ($T_h = 0.69$). Brown trout functional response to variable abundances of Chinook salmon parr ($g \cdot ha^{-1}$) was statistically significant ($N_e = 0.0009X - 0.113$; $r^2 = 0.49$; $F_{1,11} = 10.723$) (Figure 3.13).

Based on my management manipulation scenarios using the functional response models, removal of walleyes (while keeping abundance of hatchery trout constant) would decrease survival of Chinook salmon parr by up to 50.7% (Table 3.3). In fact, Chinook parr survival appeared to be correlated with walleye abundance; lower walleye abundance (i.e., higher rates of removal) led to lower Chinook parr survival. Removal of up to 50% of mean rainbow trout abundance did not influence Chinook parr survival. When all rainbow trout were removed, however, Chinook parr survival decreased considerably provided that brown trout were present. Removal of brown trout always led to increased survival of Chinook salmon parr in the Muskegon River, regardless of walleye abundance (Table 3.3). Two conditions led to an especially high increase in Chinook parr survival above baseline: 1) parr survival increased by up to 23.4% when brown trout were removed but walleyes were not and 2) parr survival increased by up to 49% when walleyes were removed and when brown trout were completely eliminated.

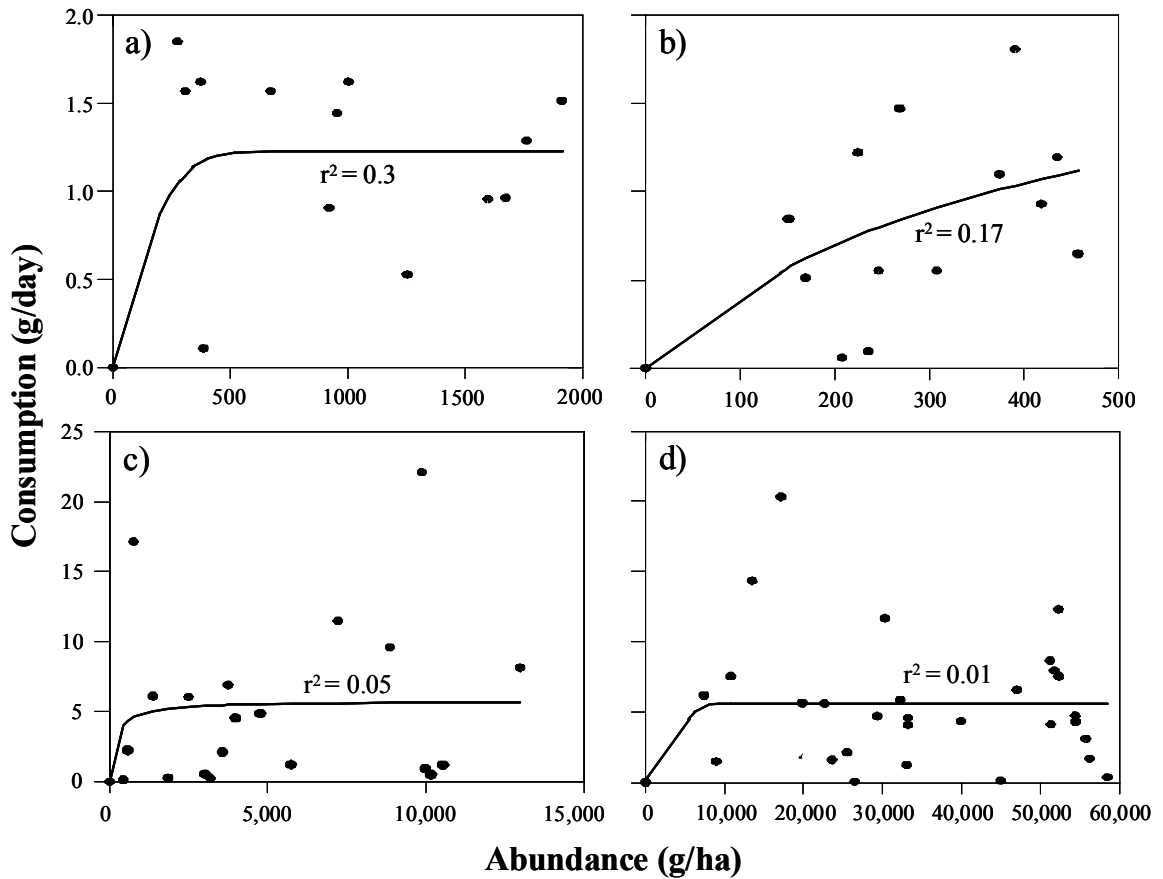


Figure 3.12. Functional response of walleyes to variable abundance of **a)** Chinook salmon parr, **b)** Cyprinidae, **c)** brown trout and **d)** rainbow trout in the Muskegon River. Solid lines indicate the functional response curve (Holling's Type II) fitted to the empirical data using least squares. Note the change in scale of axes among panels.

Table 3.2. Estimated values for the attack coefficients (a) and handling times (T_h , hours) for a multiple species functional response model (Abrams 1987) for walleyes on various prey in the Muskegon River, Michigan.

Prey species	a	T_h
Chinook salmon parr	0.49	0.43
rainbow trout	145.1	0.17
brown trout	0.03	0.17
Cyprinidae	1.37	0.69

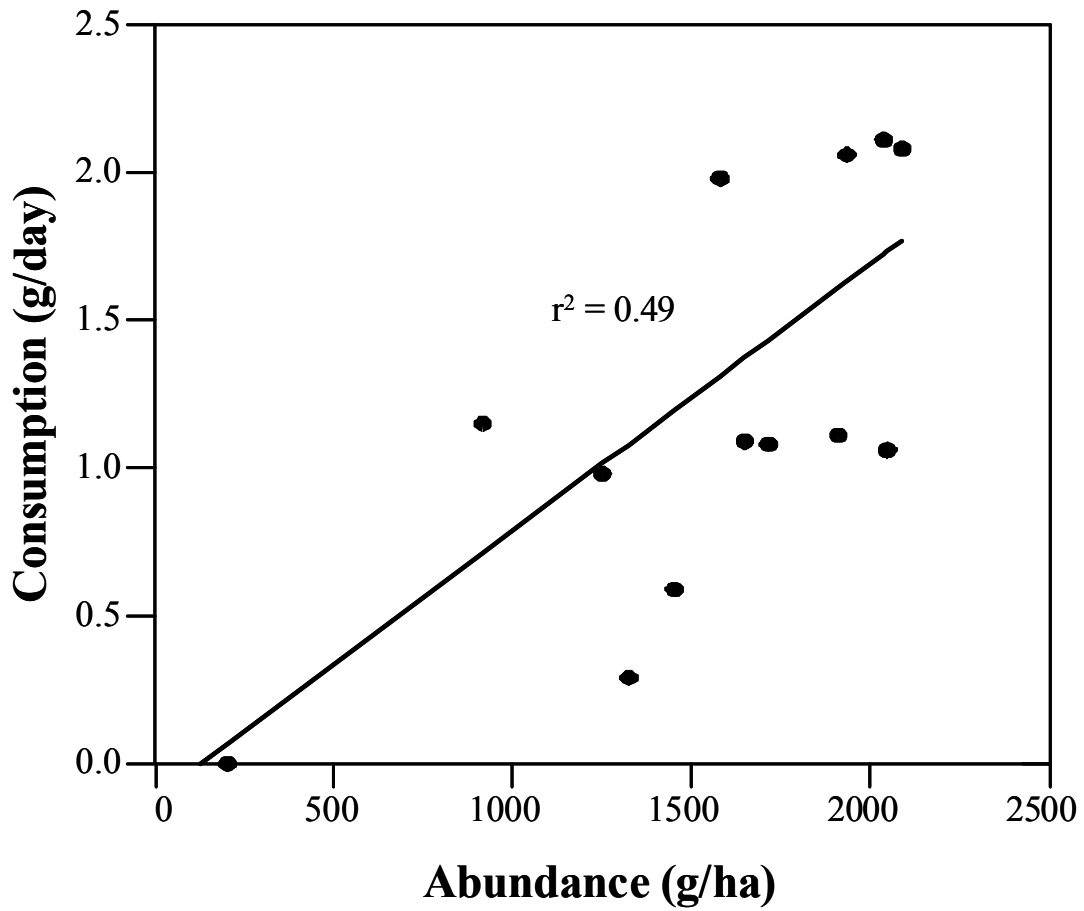


Figure 3.13. Functional response of brown trout to variable abundance of Chinook salmon parr in the Muskegon River. The solid line represents the Type-I functional response curve fitted to the empirical data.

Table 3.3. Changes in survival (abundance) of Chinook salmon parr predicted by functional response models for interactions amongst walleyes, brown trout and rainbow trout. Numeric values represent the percent change (and direction of change) in survival of Chinook parr compared to baseline ($S = 0.51$; Chapter 2). “BRT” represents brown trout and “RBT” represents rainbow trout.

	RBT-0%*	RBT-25%	RBT-50%	RBT-100%
No reduction in walleye abundance				
BRT-0%*	0**	-1.8	-2.2	-6
BRT-25%	+5.9	+4.8	+3.6	-0.6
BRT-50%	+11.7	+10.6	+9.3	-1.1
BTR-100%	+23.4	+22.2	+20.5	-3.9
25% reduction in walleye abundance				
BRT-0%	-12.6	-13.7	-14.3	-17.2
BRT-25%	-8.9	-9.8	-10.7	-13.9
BRT-50%	-5.2	-6.3	-7.3	-10.5
BRT-100%	+26.3	+24.9	+23.6	-2.9
50% reduction in walleye abundance				
BRT-0%	-25.4	-26.3	-26.5	-28.4
BRT-25%	-17.9	-18.5	-19.1	-21.2
BRT-50%	-10.5	-11.2	-11.8	-14
BRT-100%	+27.5	+27.6	+26.8	-2
100% reduction in walleye abundance***				
BRT-0%	-50.7	-50.7	-50.7	-50.7
BRT-25%	-38	-38	-38	-38
BRT-50%	-25.3	-25.3	-25.3	-25.3
BRT-100%	+49****	+49	+49	+49

*Percentage displayed represents percent reduction in abundance (e.g., BRT-25% represents 25% reduction in population size).

**Baseline, e.g., walleyes, brown trout, and rainbow trout at zero reduction in abundance.

***Without walleyes, there are no interactions with rainbow trout.

****Without walleyes or brown trout, I assumed no predation from other species.

Discussion

Predator Feeding Behavior

Walleyes are apex predators in the Muskegon River and may forage optimally unless the forage base is inadequate (Hodgson and Kitchell 1987). Walleye consumption of large brown trout and rainbow trout appeared to support my expectations of optimal foraging as larger prey are often considered more profitable than the consumption of smaller prey (Werner and Hall 1974; Kaufman et al. 2006). Further, Diana (2006) found that diets of Muskegon River walleyes were dominated by brown and rainbow trout (by weight) in 2004 and 2005 and that trend continued within and among all study years in my expanded analysis of Muskegon River predators. Although larger prey species are normally less abundant than smaller prey (Rasmussen 1993), brown trout and rainbow trout were stocked at high levels in the Muskegon River, thereby minimizing the expected discrepancy in search and handling times for large versus small prey. The large size of brown and rainbow trout prey may further minimize the relative importance of prey abundance (Kerr 1971). These assumptions are reasonable as total rainbow trout and brown trout biomass was, on average, 49 times greater than Chinook parr biomass.

Walleyes consumed rainbow and brown trout that were smaller than the average length of trout in the environment, which supports the suggestion of Juanes (1994) that piscivores select for small-sized prey independent of predator size. In Wisconsin lakes and in Lake Erie, walleyes selected prey that had similar prey/predator length ratios found in my study (range 0.2 to 0.3; Parsons 1971; Campbell 1998). Forney (1974) also showed that walleyes preferred small prey (i.e., < 20% prey/predator length), although this may have been caused by low abundance of larger forage.

Interestingly, walleyes positively selected for rainbow trout in multiple months but selected against brown trout, despite the species' similar size and morphology. This feeding behavior always occurred in June when brown trout abundance was very low. Hence, negative selection may be attributable to compensatory consumption rates by walleyes due to lower-than-expected encounter rates with brown trout. However, since handling times for rainbow and brown trout are the same but walleye attack rates on these species are highly divergent, other important differences must exist between the two prey types. Piscivorous brown trout were found in very shallow water 1.5 times more frequently than rainbow trout, perhaps searching for Chinook salmon parr (D. Krueger unpublished CPUE data). Rainbow trout, however, were found in the middle of the river or in plunge pools about six times more frequently than brown trout, feeding on invertebrates in the drift. Walleyes also were captured in deeper, faster moving water. The opposing foraging strategies of brown trout and rainbow trout may therefore have led to higher spatial overlap between walleyes and rainbow trout and may explain the asymmetric predation rates I observed in walleyes.

Spatial overlap between walleyes and Chinook parr also must have been very low due to the extremely shallow water in which parr were found. Hence, walleye consumption of Chinook salmon parr was relatively low compared to brown trout piscivory. Walleyes never selected for Chinook salmon parr and actually selected against parr in three of four study years. In addition, I found no relationship between walleye size and Chinook parr size. Few walleyes (of any size) consumed Chinook salmon parr in any given year. Walleye feeding behavior was similar in Lake Huron, where they preferred larger alewife prey over smaller Chinook smolts (Johnson et al. 2007). In the

Muskegon River, walleyes and Chinook parr generally do not exhibit high spatial overlap (Chapter 2). Even so, the small size of Chinook salmon parr may prevent them from entering the perceptual field of walleye, thereby leading to lower encounter rates relative to hatchery trout (Gerritsen and Strickler 1977). The relatively low attack rate coefficient of walleyes on Chinook parr supports this claim while the high handling time is likely an artifact of fitting the model as walleyes should be able to easily handle or evacuate Chinook prey. The few walleye that consumed large numbers of Chinook salmon parr may have responded to transient dense patches of prey (Petersen and DeAngelis 2000). Inclusion of these piscivores in my analysis likely skewed mean consumption of Chinook salmon parr by walleyes towards the high end.

Muskegon River walleyes appeared to respond quickly to changes in prey densities and exhibited prey-switching behavior twice per sampling season. First, although walleyes did not eat for the first few weeks in the river (i.e., March – early April) when they were actively spawning, they began feeding by mid April after spawning when trout were first stocked. Brown and rainbow trout were stocked at boat launches and were patchily distributed near boat launches throughout the early spring (April – May). Walleyes that consumed brown and rainbow trout were generally found aggregated near these boat launches but walleyes that consumed other prey items were more isolated (i.e., walleyes were captured one at a time) (D. Krueger University of Michigan unpublished data). Based on daily rations and attack coefficients, it is apparent that once walleyes began to feed, they preferred to consume rainbow trout. The artificially high densities of stocked trout likely elicited the observed walleye feeding response (Lyons 1987; Petersen and DeAngelis 1992; Baldwin et al. 2003). The second

prey switch occurred late in the sampling season. Following the departures of preferred (rainbow trout) and alternate (Chinook salmon parr) prey species, walleye predation on Cyprinidae increased in three of four study years. Walleyes that remained in the river continued to prey upon Cyprinidae into July and August (D. Krueger University of Michigan unpublished data).

Brown trout are typically piscivorous at sizes of 300 mm TL or greater (Keeley and Grant 2001), but I found high rates of piscivory in much smaller individuals (TL ~ 164 mm). This result is perhaps not surprising given the high abundance of small Chinook salmon parr (Kahilainen and Lehtonen 2002). While 30% of brown trout diets contained Chinook salmon parr, it appeared that brown trout selected the smallest available parr. I noticed an especially high rate of piscivory and positive selection for Chinook salmon parr in April (2006) presumably due to the small size of parr (mean TL 39 mm) which was 24% of brown trout length. In May, mean Chinook parr length (46 mm TL) was about 28% of brown trout length, selection for Chinook was lower (neutral) as was the proportion of brown trout ration that was composed of Chinook parr. The mean size of ingested Chinook parr, however, was always significantly less than the environmental mean. By June, Chinook parr length (53 mm TL) was ~32% of brown trout length, and although the theoretical gape limit of the average brown trout was higher (~40%; Damsgård 1995), I never observed brown trout predation on parr > 46 mm. Further, I observed only three instances of brown trout consuming Chinook with prey/predator length ratios > 26%, my estimated maximum value. Maximum prey size was likely dictated by the increase in handling time that a larger prey item represented.

Therefore, the maximum prey/predator ratio found in my study is probably more realistic than that of Damsgård (1995) due to its functional applicability.

Given the relatively small gape of brown trout, Chinook growth may be a useful predictor of Chinook parr survival. Chinook salmon parr inhabit the Muskegon River for approximately 60 days, and since they can reach 50 mm within 40 days of emergence (Chapter 2), it appears they can attain a size refuge from brown trout well before out-migration. Rapid growth would therefore reduce parr vulnerability to predation throughout the latter portion of the nursery-dependent life stage (e.g., Chapter 2). Hence, hatchery brown trout may impose high predation rates on Chinook salmon parr only in the early spring when parr are less than 40 mm and appear to be most vulnerable.

Brown trout preyed explicitly upon Chinook salmon parr during the short temporal overlap with suitably small individual prey. Still, in May and June, invertebrate prey became an increasingly large component of brown trout diets. Some invertebrate taxa (Ephemeropterans in particular) may have experienced large emergence events during this time although I did not have sufficient data to detect changes in invertebrate biomass over time. Hence, I cannot discount the possibility that brown trout predation on Chinook parr also was influenced by changes in invertebrate abundance.

Functional Response and Management Implications

The functional response I observed for walleyes in the Muskegon River was similar to predatory responses observed in other field and laboratory studies of walleyes (Forney 1974; Swenson 1977) and other piscivorous fishes (Ruggerone and Rogers 1984; Fresh and Schroder 1987). Fresh and Schroder (1987) reported that the foraging behavior of stream salmonids on variable abundances of juvenile chum (*O. keta*) fit a Type II pattern.

Further, salmonids responded rapidly (< 48 hours) to variable abundances of released chum in small stretches of natural (1.5 – 2.3 km) and artificial (33 m) streams. The Type-I functional response by brown trout to variable prey abundance in the Muskegon River (nursery = 22.5 km) indicates that this predator may not be satiated by the abundances of Chinook salmon parr I observed. Consequently, I used bioenergetic simulations (Krueger et al. unpublished data) to calculate the maximum daily consumption rate (C_{\max}) by an average brown trout (164 mm TL) of $3.2 \text{ g} \cdot \text{day}^{-1}$. According to my foraging model, this level of consumption is predicted at a Chinook parr density of approximately $3,700 \text{ g} \cdot \text{ha}^{-1}$ which is about 1.8 times the typical initial (i.e., maximum) abundance of Chinook parr in the Muskegon River. Thus, it seems brown trout are capable of consuming an even larger number of available Chinook salmon parr compared to what I observed.

Many studies have described feeding responses of walleyes and brown trout (e.g., Swenson and Smith 1973; Ringler 1979; Porath and Peters 1997; Elliott and Hurley 2000), though several of them were performed in controlled laboratory settings using only one prey type. My foraging model used empirically derived data to describe the feeding behavior of predators to varying densities of prey. Further, I considered variable densities of three prey types in my analysis to describe walleye feeding behavior. Since I did not perform laboratory trials to accurately determine attack rate coefficients (a_i) and handling times ($T_{h,i}$), my functional response curves had relatively low fit. Still, my model predicted attack coefficients that supported the observed trends in predator ration, prey selection and consumption and implicitly included differences in the spatial overlap of predator and different prey types. My handling time estimates also support observed trends in feeding behavior although their estimation may be unnecessary as handling

times are relatively unimportant for piscivores (Breck 1993). Evacuation rates may be more important than handling times for piscivores, and evacuation rates are primarily dependent on temperature (Swenson and Smith 1973; Wahl and Nielsen 1985; He and Wurtsbaugh 1993). Because temperature is easily determined, evacuation rates may be easier to estimate than handling times. Therefore, due to its relative simplicity in terms of data collection and application, my foraging model may serve as a more realistic and readily utilized management tool for tributaries in the Great Lakes and Pacific Coast regions.

Harvey and Kareiva (2005) recommended that a targeted removal of predator species was the most effective way to reduce predation on salmon smolts. Removal of walleyes, brown trout, or rainbow trout in the Muskegon River can easily be accomplished by cessation of stocking efforts. My foraging model simulations may therefore provide useful predictions of scenarios that result from stocking manipulations. Although removal of walleyes would be difficult to achieve from a practical perspective, this simulation was worthwhile as it highlighted the importance of walleyes as a mediator of Chinook parr vulnerability to predation from brown trout. Removing walleyes would lead to increased brown trout abundance due to the lack of predation mortality from walleyes and a net increase in predation mortality on Chinook salmon parr. Each scenario that involved removal of rainbow trout resulted in reduced survival of Chinook salmon parr (Table 3.3). Thus, rainbow trout must positively (and indirectly) influence survival of Chinook salmon parr by buffering predation via walleyes (e.g., Chapter 2). In Oneida Lake, the abundance of alternate forage (mayflies, yellow perch) was similarly influential to walleye cannibalism of their young (Forney 1974; Rose et al. 1999). On the

other hand, all scenarios with reduced brown trout abundance led to increased survival of Chinook salmon parr. Although brown trout may also provide an indirect benefit to Chinook parr via buffering predation mortality by walleyes, this benefit is outweighed by their direct predatory impact on Chinook parr survival. Thus, termination of non-indigenous brown trout stocking efforts would greatly improve survival rates of Chinook salmon parr.

Removal of a particular prey type (i.e., brown trout) would require assumptions to determine the subsequent diet composition of a predator. In the Muskegon River, walleyes would be expected to consume artificially high levels of Chinook prey to compensate for the caloric deficit previously satisfied by the missing prey. Thus, it is important to consider predator feeding behavior and prey preference (Anderson et al. 2005) when implementing management plans to remove or control the abundance of a particular species.

Several factors may have contributed to the relatively poor fit of the walleye functional response models to observed data. First, predator and prey abundances in the Muskegon River generally decreased throughout each sampling year due to seasonal migrations. Next, my study site (22.5 km) was much larger than other study sites (33 m to 2.3 km; Ruggerone and Rogers 1984; Fresh and Schroder 1987) which may have precluded my ability to collect sufficient diet data. Finally, I observed predator feeding behavior for nearly three months while most studies only did so for several hours or days. Predation rates are highly variable for fish in natural habitats, thereby making functional response curves difficult to plot (Peterman and Gatto 1978; Fresh and Schroder 1987). These factors may have combined to limit my ability to accurately depict predator

foraging responses to variable prey abundance. Swenson (1977) reported a stronger relationship between walleye consumption and prey densities for two Minnesota Lakes and Lake Superior. The plotted values, however, were compiled for all three lakes and represented monthly averages and likely dampened the high variability in predation rates compared to my observations of migratory riverine fishes.

My empirical data represented daily averages and showed that predator consumption rates can be much higher or much lower than my functional response relationships predicted. Consider the simulation where all brown and rainbow trout were removed and Chinook survival only decreased by 3.9%. In reality, this type of manipulation would likely lead to one of several possible outcomes including: 1) fewer walleyes would remain in the river post-spawn, or 2) walleye feeding behavior would change and consumption of Chinook parr would increase substantially more than my model suggested. I was unable, however, to simulate either of these scenarios. Although walleye functional responses exhibited poor fit to observed data, brown trout foraging response to variable Chinook parr abundance in the Muskegon River exhibited a better fit and was similar to that of Fresh and Schroder (1987) in a closed, artificial stream. Hence, my model may be broadly applicable as it was parameterized with reliable empirical data (Chapter 2) that independently yielded similar results to the foraging model presented here.

Muskegon River fishery managers have the ability to control species interactions through stocking efforts. Hence, manipulating the abundance of important sport fishes, especially trout, can quickly improve survival and recruitment of Chinook salmon. In this sense, the Muskegon River is a model system for other Great Lakes and Pacific Coast

tributaries that rely on production of salmonid recruits. Provided that tributary managers have the goal of efficiently increasing Chinook salmon recruitment in order to sustain adult stocks, I recommend elimination of brown trout stocking in tributaries that produce Chinook salmon parr. Management efforts directed at controlling walleye abundance should be discouraged as long as brown trout are stocked into the Muskegon River. Further, such management efforts are probably unnecessary due to the relatively low predation rates of walleyes on Chinook parr when hatchery rainbow trout are present.

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Chapter IV

Modeling the Impact of Alternate Management Strategies on Chinook Salmon Population Dynamics in a Large Lake Michigan Tributary

Abstract

Chinook salmon experience variable recruitments throughout their native and introduced ranges that may be caused by predation on smolts by stocked predators in tributary streams. I used a stage-based matrix model (RAMAS), parameterized with empirically-derived data, to simulate impacts of predation by walleyes and brown trout on Chinook salmon recruitment and population growth rate from the Muskegon River tributary to Lake Michigan. Key parameters of the model included stage-specific estimates of Chinook salmon growth, survival, abundance and fecundity. I simulated effects of predators on survival rates of Chinook salmon during the fry-to-smolt stage and observed the long-term effects on Chinook salmon recruits and population growth rate. All other stage-specific values were held constant in predation scenarios. I also simulated effects of environmental stochasticity on Chinook salmon fecundity, recruitment and population growth by increasing variation around all model parameters and reducing egg-fry survival rates. Relative to a baseline scenario of low stochasticity, median egg-hatch survival and mean size at age of adults, only the removal of brown trout resulted in a

significant increase in long-term (≥ 50 years) Chinook salmon recruitment. Similarly, long-term population growth of Chinook salmon increased only when brown trout abundance was low or absent. Predation on Chinook salmon smolts during out-migration was positively correlated with variation in salmon population growth. Fishery management decisions on Chinook salmon management should therefore be informed by potential tradeoffs involving stocked predators.

Introduction

Variation in recruitment of Chinook salmon (*Oncorhynchus tshawytscha*) from natal tributaries can be attributed to the effects of abiotic and biotic factors which affect survival and growth of early life stages (Hilborn and Walters 1992; Shively et al. 1996; Jager et al. 1997; Johnson et al. 2007). In many Pacific Coast and Great Lakes tributaries, variability in Chinook salmon recruitment (number of smolts entering the lake or ocean; Jager and Rose 2003) is mediated through management actions (Chapter 2, 3) in the riverine nursery area. Stocked piscivores may prey heavily on Chinook salmon parr, potentially leading to high mortality rates on juvenile stages (e.g., Rieman et al. 1991; Johnson et al. 2007, Chapter 2).

Previous studies (Chapters 2, 3) explored the potential for management actions to increase survival of Chinook salmon parr over four field seasons in the Muskegon River, a large Lake Michigan tributary. These empirical studies (Chapters 2, 3) found that potential recruitment of Chinook salmon was heavily affected by piscivory from walleyes and brown trout. Alternate forage such as hatchery-reared rainbow trout (*O. mykiss*), however, may provide a significant buffer to predation mortality on Chinook parr. Analysis of piscivore feeding behavior documented species-specific predation on Chinook salmon parr as well as important indirect interactions between Chinook salmon parr and alternate prey species (Chapter 3). The extent of manipulation or control of predator-induced mortality in these studies, however, was minimal. Studies have shown that by manipulating fishing and stocking regulations, fishery managers can influence predator-prey interactions and hence, the population dynamics within a system on a short temporal scale (< 10 years; e.g., Krueger and Hrabik 2005).

In this study, I simulated the effects of longer-term (i.e., > 10 years) management manipulations of species composition and interactions on Chinook salmon dynamics in Lake Michigan (Harvey and Kareiva 2005). The objective of this paper was to assess the relative impacts of stocked predators on Chinook salmon recruitment and population size. I hypothesized that predation during the short nursery period of 1 – 2 months has significant impacts on variability in Chinook salmon recruitment and population growth rate. To test this hypothesis, I simulated the effects of predation on Chinook population dynamics using a stage-based matrix model, parameterized to approximate the Chinook salmon population in the Muskegon River and Lake Michigan.

Methods

Modeled Ecosystem

My model incorporated all life stages of Chinook salmon so I considered influential processes in three major habitats: the Muskegon River, Muskegon Lake and Lake Michigan (Figure 4.1). The Muskegon River is especially important as it produces more wild Chinook salmon smolts than any other Lake Michigan tributary (Carl 1984; O’Neal et al. 1997). Wild produced Chinook salmon smolts are more economically efficient than hatchery smolts because they are essentially free (hatchery smolts require months of rearing) and they do not require a caged “imprinting” period. The sport fish populations in the Muskegon River are supported by stocking predators including walleyes (*Sander vitreus*) and brown trout (*Salmo trutta*), and insectivorous rainbow trout. Muskegon Lake is a 1,680 hectare drowned river mouth of the Muskegon River that connects to southeastern Lake Michigan via a navigation channel (Muskegon Channel). Muskegon Lake is relatively shallow and mesotrophic and provides a temporary residence for

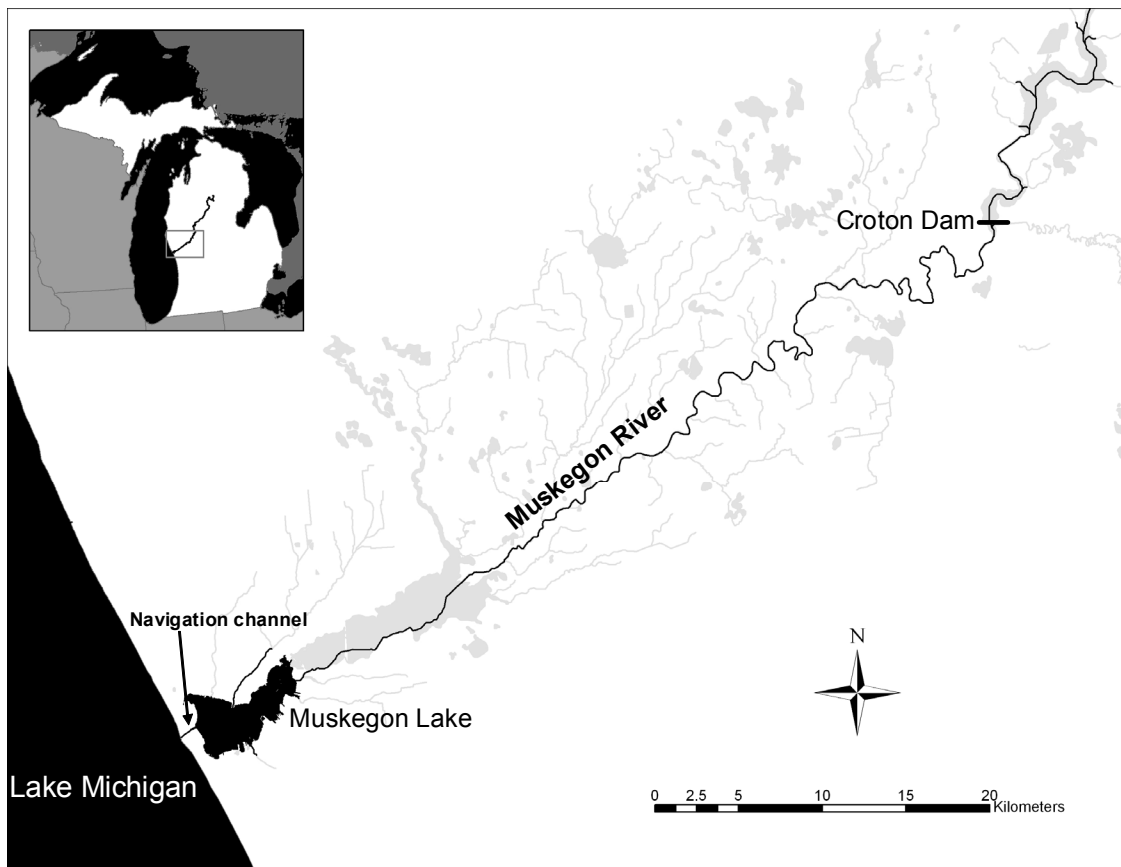


Figure 4.1. The location of the modeled ecosystem, showing the three major habitats for Chinook salmon in the Muskegon River Estuary System: Muskegon River, Muskegon Lake and Lake Michigan.

Chinook parr before they complete their out-migration into Lake Michigan. Lake Michigan, the second largest Laurentian Great Lake (58,016 km²), provides important habitat and forage for growing juvenile and adult Chinook salmon.

Modeling Approach

I used RAMAS Stage (Ferson 1993) to evaluate alternative predator management strategies affecting the early life history stages and how they might affect population dynamics of Chinook salmon. RAMAS Stage is a matrix modeling approach developed for understanding population dynamics of species with complex life histories. This program tracks the number of individuals in each stage (Caswell 2001), allowing researchers to forecast population trajectories based on minimal demographic data such as survival, growth and reproduction (Brook et al. 1999; Sable and Rose 2008). Model simulations may also implicitly include environmental factors such as river and lake water temperatures, and river discharge that may affect survival and growth of salmon life stages and hence salmon population dynamics. I configured RAMAS Stage to simulate finite stages describing the life cycle of Chinook salmon. Model simulations began with an initial abundance of Chinook salmon at each age or stage. Individuals that survived one stage moved into the next stage based on field-derived transition probabilities.

Data Sources and Baseline Simulation

I parameterized the RAMAS Stage model using stage- specific abundances, survival rates, and fecundities of Chinook salmon (Table 4.1). My RAMAS Stage matrix included 7 life stages of Chinook salmon: fry and smolts in Muskegon River, and ages 0 through 4 in Lake Michigan. The river-fry stage represents Chinook just after emergence

Table 4.1. Stage matrix used in the baseline simulation. Off-diagonal values represent stage-specific survival rates while top row elements represent stage-specific fecundity values (# of river-fry individuals per female).

	River		Lake				
	fry	smolt	0	1	2	3	4
River-fry			0	0.026	0.601	8.336	15.939
River-smolt	0.51						
Lake-0		0.750					
Lake-1			0.705				
Lake-2				0.705			
Lake-3					0.350		
Lake-4						0.259	

from redds in early April. One or two weeks after hatching, fry quickly deplete their yolk reserves and become parr. Approximately two months later (June), parr will enter the river-smolt stage, at which point they will out-migrate toward Lake Michigan, a process that generally takes one to two days. Smolts that reach Lake Michigan are considered to enter the lake-0 stage. Individuals enter stages lake-1 to lake-4 one year after entering the previous stage. Abundance and survival rates of Chinook salmon were obtained from empirically-derived predation mortality rates from walleyes and brown trout in the Muskegon River and stocking evaluations of salmon in Lake Michigan (Rutherford 1997; Benjamin and Bence 2003) while fecundity values were obtained from the literature.

Survival Rates: Fry to smolt survival rates were based only on predation mortality and were estimated using a multi-species functional response algorithm based on field and modeling studies of foraging behavior of walleyes and brown trout in the Muskegon River (Chapters 2, 3). This value changed markedly across simulations as it was dependent on walleye, brown trout and rainbow trout abundance (and therefore predation rates). Survival values for adult lake stages were held constant and were based on analyses of Chinook salmon density and age composition in biological surveys and creel data compiled for a deterministic catch-at-age model (“CONNECT”) that predicts fishery yield as a function of stocking abundance (Rutherford 1997; Benjamin and Bence 2003). Natural mortality rates (including spawner mortality) of lake-phase salmon ranged from 27% at age-1 to 53% at age 4; not all individual Chinook survive to spawn. Natural mortality was assumed to be age-specific and constant. Finally, for all simulations, I implemented a 50% angler harvest rate for the age 1 – 4 spawners. Creel estimates from the 1980s and 1990s show that 20,000 – 40,000 spawners were harvested annually from

the Muskegon River which supports my harvest assumption (Michigan Department of Natural Resources unpublished data).

Abundances: Since Chinook salmon are no longer stocked into the Muskegon River, I used estimates of mean abundances of fry (541,272) and smolt (291,232) production from 2004 – 2007 (Chapter 2) as the initial fry and smolt abundances. Initial abundances of lake stages were based on age composition data from agency surveys in Lake Michigan and creel surveys and research surveys from the Muskegon River (Table 4.2; D. Krueger University of Michigan unpublished data).

Fecundity: Several calculations were required in order to determine Chinook salmon fecundity, which I defined as the number of river-fry individuals produced per adult Chinook salmon. I first estimated egg deposition based on a length-specific relationship averaged for 10 spawning populations of Chinook salmon in the Pacific Northwest (Healey and Heard 1984):

$$F = 0.00195 \cdot L^{2.234} \quad (1)$$

where F is the number of eggs deposited by each female and L is total length (mm).

Next, I estimated the number of spawning females using spawning mortality estimates and a maturity schedule (Table 4.3) and assumed a 1:1 sex ratio and 50% harvest rate:

$$female_{lake-i} = P_f * Mature_i * A_{lake-i} * \sum_{i=1}^4 PE_{lake-i} \quad (2)$$

where $female_{lake-i}$ is the abundance of female spawners in stage i , P_f is the product of the proportion of females and the harvest rate ($0.5 * 0.5 = 0.25$), $Mature_i$ is the fractional contribution of stage i to total spawner abundance, A_{lake-i} is the proportional mortality in stage i due to spawning (lake-1 = 0.02, lake-2 = 0.1, lake-3 = 0.6, lake-4 = 0.8) and PE_{lake-i} is the initial abundance of stage i . I then multiplied stage-specific female

Table 4.2. Initial stage-specific abundances of Chinook salmon used in modeling scenarios.

Stage	Initial Abundance
Fry	541,272
Smolt	291,232
Lake-0	218,424
Lake-1	153,770
Lake-2	108,254
Lake-3	37,878
Lake-4	9,818

Table 4.3. Maturity schedule (stage-specific contribution to total spawner abundance) for Chinook salmon in Lake Michigan as a function of relative alewife biomass. Age composition data were available from spawners sampled at the Little Manistee River weir (Randy Claramunt Michigan Department of Natural Resources personal communication). Age 5 fish were not included in my analysis as they are a minimal component of harvest (Johnson et al. 2005).

Age	% of total spawner abundance		
	baseline	LOW alewife	HIGH alewife
Lake-1	3.6	0	6.9
Lake-2	20.4	5.7	47.2
Lake-3	54.8	60	37.6
Lake-4	20.9	31.4	8.3
Lake-5	0.2	2.9	0

spawner abundance by individual female egg production and divided that value by the summation of all eggs produced by all stages to determine stage-specific egg production:

$$Egg_{lake-i} = \frac{F * female_{lake-i}}{\sum_{i=1}^4 (F * female_{lake-i})} \quad (3)$$

where Egg_{lake-i} is the proportional contribution of stage i toward total egg production.

Finally, I calculated stage-specific fecundity of all individuals by assessing the contribution of all salmon in each stage toward total egg production and multiplied that by survival from the egg to fry stage:

$$Fecundity = \frac{Egg_{lake-i} * S_{fry}}{PE_{lake-i}} \quad (4)$$

where S_{fry} is egg to fry survival and $Fecundity$ is the number of river-fry individuals per adult salmon. Egg to fry survival was 9% based on my assumptions that egg viability was 70%, egg-hatch survival was 0.85, and hatch to fry survival was 15% (Quinn 2005).

Alewives (*Alosa pseudoharengus*) are the primary prey of adult Chinook salmon in Lake Michigan (Kitchell and Crowder 1986). Hence, abundance of alewife prey in Lake Michigan may influence the growth rate (Stewart and Ibarra 1991) and the maturity schedule (Quinn 2005) of Chinook salmon. Further, variation in salmon body size changes population fecundity since fecundity is a nonlinear function of Chinook salmon length (Equation 1). A length-at-age relationship for adult Chinook salmon in Lake Michigan was estimated using an age and growth study of Lake Michigan Chinook salmon (Wesley 1996) (Table 4.4). I used estimates of length-at-age (Wesley 1996) to calculate fecundities that represented periods of high alewife abundance and large Chinook salmon size (1990s) as well as low alewife abundance and small Chinook

Table 4.4. Mean size (mm TL) of spawning Chinook salmon for baseline, LOW and HIGH alewife abundances. Changes in size at age were calculated using data from the Muskegon River and from Wesley (1996).

Age	Mean size (mm)		
	LOW	Baseline	HIGH
Lake-1	370	393	416
Lake-2	609	636	662
Lake-3	765	828	891
Lake-4	815	931	1047

salmon size (1980s) (Table 4.5). Chinook salmon that were lake age 1 and older are considered mature and therefore assigned fecundity values. Lake-4 was the oldest stage class used in my simulations as the Lake-5 stage class represents a minimal component of harvest (Johnson et al. 2005). The lake-3 stage was responsible for the majority of spawners, except when alewife abundance was HIGH (Table 4.3).

Environmental Variation: Environmental influences on variability in Chinook salmon survival (Carl 1982), fecundity and population dynamics were modeled implicitly in RAMAS Stage. For each simulation run, a vital rate (survival or fecundity) was selected as a random variate from a normal distribution whose mean was specified from the Stage matrix (which incorporated density dependence) and whose standard deviation was taken from the standard deviation matrix. I assumed a ‘LOW’ level of environmental variation by including a constant rate of one standard deviation around certain model parameters; one standard deviation was assumed to be 10% of mean values in the Stage matrix.

Density dependence: Population dynamics and recruitment of Chinook salmon are influenced by density dependent mechanisms in early life stages (Ricker 1954, 1975). I assumed a “ceiling” type density dependence for Chinook salmon that has been promoted in fisheries science to describe population dynamics of various species such as Coho salmon (*O. kisutch*) (Barrowman and Myers 2000; Bradford et al. 2000). Ceiling density dependence is similar to a Ricker-type density-dependent function but simpler; the population grows exponentially until it reaches the ceiling (carrying capacity):

$$N_t = N_0 e^{rt} \quad (5)$$

where N_0 is the initial population, r is the population growth rate and t is the time in years. Exponential growth occurs if $r > 0$ and exponential decay occurs if $r < 0$. If

Table 4.5. Variation in fecundity values (number of river-fry individuals produced per female spawner) due to changes in abundance of alewife prey in Lake Michigan (modeled as change in size of adult Chinook salmon).

Stage	Fecundity		
	LOW alewife abundance	MEAN Alewife abundance	HIGH alewife abundance
Lake-1	0	0.026	0.059
Lake-2	0.172	0.601	1.619
Lake-3	8.609	8.336	7.158
Lake-4	20.022	15.939	8.741

abundance increases above carry capacity, it is set to the ceiling value (i.e., max). A population that reaches the carrying capacity will remain at that abundance until a population decline occurs through random fluctuation (i.e., demographic or environmental stochasticity). Another important difference between the ceiling type of density dependence and the Beverton-Holt (compensatory) and Ricker (over-compensatory) types is that the ceiling does not assume that a population will recover from low densities (Sabo et al. 2004). When the population is below its carrying capacity, the likelihood that the population grows or declines at any time step is entirely dependent on the Stage Matrix and its variation (Standard Deviation Matrix). I specified a carrying capacity (K) of 2 million individuals to accommodate the initial abundance of Chinook salmon (1.36 million for all stages combined) and allow for potential population growth.

Model Simulations

Baseline simulation: I used a mean survival rate of $S = 0.51$ for Chinook salmon parr under mean values of walleye and brown trout abundances (walleye = 3,027; brown trout = 24,283 individuals) from 2005 – 2007 (Chapter 2) to estimate the baseline value of Chinook salmon recruitment (number surviving to lake-0 stage), adult abundance and risk of population decline. The abundance of predators used in modeling simulations reflected the number that actually consumed Chinook parr, which was lower than the abundances of spawning walleyes (~38,000) or stocked brown trout (~86,000). The baseline simulation also incorporated mean values of fecundity and sizes-at-age of adult Chinook salmon. In addition, I assumed a LOW level of environmental stochasticity by placing a one-standard deviation boundary around all model parameters.

Predator Management scenarios: I first characterized the potential effects of variable predator abundance on Chinook salmon population dynamics by varying the survival rate from the fry to smolt stage (Table 4.6). I ran absence and presence scenarios for walleyes and brown trout, singly and in combination (ABSENT, LOW, MEAN, HIGH; Table 4.7), given relative abundances of alternate forage species (Cyprinidae, brown trout, rainbow trout) for walleyes (Table 4.6). For walleye forage, I added a simulation that excluded rainbow trout but included remaining forage species (Cyprinidae, brown trout), and another that excluded Cyprinidae (removed indirect effects from minnows) (Table 4.6). Cyprinidae were otherwise included as prey in all simulations. A simulation to represent no predation (walleyes and brown trout ABSENT) was run to yield theoretical maximum recruitment and population growth rates.

I ran additional simulations to determine the potential for environmental stochasticity to influence Chinook salmon recruitment rates. The riverine-dependent stages of the Chinook salmon life cycle are more likely to be influenced by environmental variation since survival from egg to hatch is almost entirely dependent on environmental conditions (Quinn 2005; Honea et al. 2009; Jensen et al. 2009). Further, riverine conditions fluctuate more widely than conditions in Lake Michigan. Therefore, I only imposed the increased levels of environmental variation on riverine survival (i.e., fry survival, parr survival) and adult fecundity. I increased environmental stochasticity by increasing variation around fecundity and parr survival estimates from one standard deviation to two (MODERATE) and five (HIGH) standard deviations. The influence of

Table 4.6. Experimental design for the matrix model simulations. Numeric values represent survival of Chinook salmon parr predicted from a functional response model (Chapter 2) for each simulation. Baseline recruitment was achieved using MEAN abundance of walleye and brown trout, LOW environmental stochasticity, mean alewife abundance and 60% egg-hatch survival (Quinn 2005).

Simulation	Chinook parr survival
WE ABSENT	
BRT ABSENT	1
BRT LOW	0.85
BRT MEAN	0.64
BRT HIGH	0.24
WE LOW	
BRT ABSENT	0.99
BRT LOW	0.85
BRT MEAN	0.58
BRT HIGH	0.23
WE MEAN	
BRT ABSENT	0.91
BRT LOW	0.77
BRT MEAN	0.51
BRT HIGH	0.15
NO hatchery trout	0.64
WE HIGH	
BRT ABSENT	0.8
BRT LOW	0.68
BRT MEAN	0.41
BRT HIGH	0.06
WE MEAN, BRT MEAN	
NO Cyprinidae	0.44
LOW alewife abundance	0.51
HIGH alewife abundance	0.51
Environmental Stochasticity MODERATE	0.51
Environmental Stochasticity HIGH	0.51
WE HIGH, BRT HIGH	
Environmental Stochasticity MODERATE	0.06
Environmental Stochasticity HIGH	0.06
WE ABSENT, BRT ABSENT	
Environmental Stochasticity MODERATE	1
Environmental Stochasticity HIGH	1

Table 4.7. Predator abundance at ABSENT, LOW, MEAN and HIGH designations

Predator	Abundance			
	ABSENT	LOW	MEAN	HIGH
Walleye	0	984	3,027	6,820
Brown trout	0	10,927	24,283	55,851

environmental stochasticity was simulated in combination with low (0.06), mean (0.51) and high (1.0) fry-smolt survival rates. I assumed a high (100%) survival rate in the absence of walleye and brown trout predation to investigate the relative influence of predation on Chinook salmon recruitment dynamics; walleyes and brown trout were the only significant predators of Chinook parr in the Muskegon River.

Finally, I examined the effects of alewife abundance on body size, age at maturity and population dynamics of Chinook salmon by varying Chinook salmon fecundities as a function of altered adult growth rates and maturity schedules (Table 4.5).

Model Output: All simulations were replicated ($n = 50$) and run for 50 years. For each simulation I reported mean recruitment (abundance of Chinook salmon at lake-age 0), population abundance (mean adult abundance of the final 10 years in each simulation) and the probability that the adult population would fall below one-third of initial adult abundance (103,230) which may be considered a “healthy” population (e.g., Jager and Rose 2003). Results from all model simulations are reported as % mean deviation from baseline conditions, with 95% confidence intervals at $\alpha = 0.05$ and d.f. = 49. Differences between simulation results and baseline conditions were considered significant if their 95% confidence intervals did not overlap. I reported coefficients of variation (CV) for recruitment and population abundance for the last 10 years of each simulation to quantify variability. Finally, I define that a particular scenario resulted in a population “crash” if the total population abundance fell below 1,000 total individuals at any point during the simulation and noted the time (in years) that the population persisted.

Results

Baseline simulations: Mean abundance of all stages of Chinook salmon remained fairly constant for the baseline 50-year simulation (Figure 4.2). The mean abundance of lake-0 Chinook salmon recruits after 50 years was 135,489 ($\pm 21,488$) (Figure 4.2a), mean abundance of adult stages was 188,490 ($\pm 30,904$) (Figure 4.2b) and the total population abundance for the final 10 years was stable at 858,245 (C.V. = 0.01), which includes all river and lake stages. The stable age distribution indicates that most adults were in the lake age-1 and 2 stages (Figure 4.2c). The population did not “crash” in any single replicate of the baseline simulation.

Management scenarios: Relative recruitment success of Chinook salmon was higher under simulated walleye-only regimes than under brown trout-only regimes. In the absence of brown trout, simulated mean recruitment to the lake-0 stage increased 161% (range 152 to 174%) compared to baseline conditions. In the absence of brown trout and rainbow trout, simulated Chinook recruitment to the lake-0 stage was approximately double that of baseline (Figure 4.3). Relative recruitment of Chinook salmon also varied inversely with relative abundance of brown trout in the absence of walleye. Relative recruitment of Chinook salmon was higher than baseline at LOW and MEAN brown trout abundance and decreased significantly below baseline at HIGH brown trout abundances (Figure 4.4).

In simulations with both walleye and brown trout present, relative recruitment of Chinook salmon was highly dependent on predator abundances. Simulated Chinook salmon recruitment increased above baseline when brown trout abundance was LOW regardless of walleye abundance. At MEAN levels of brown trout abundance, relative

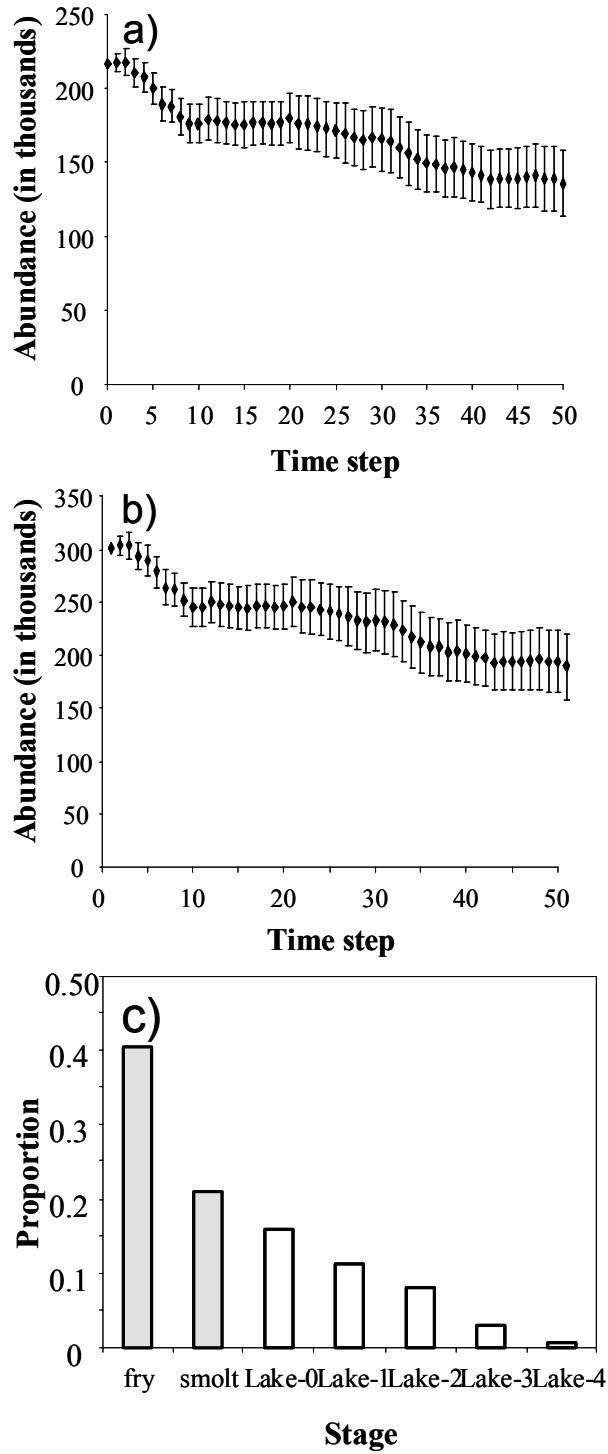


Figure 4.2 a) Population trajectory of Chinook salmon recruits, and b) population trajectory of adults for the 50-year baseline simulation. Error bars represent 95% confidence intervals based on 50 replicates. c) Stable age distribution of Chinook salmon as a proportion of total Chinook abundance resulting from the baseline scenario. The shaded bars denote the river stages.

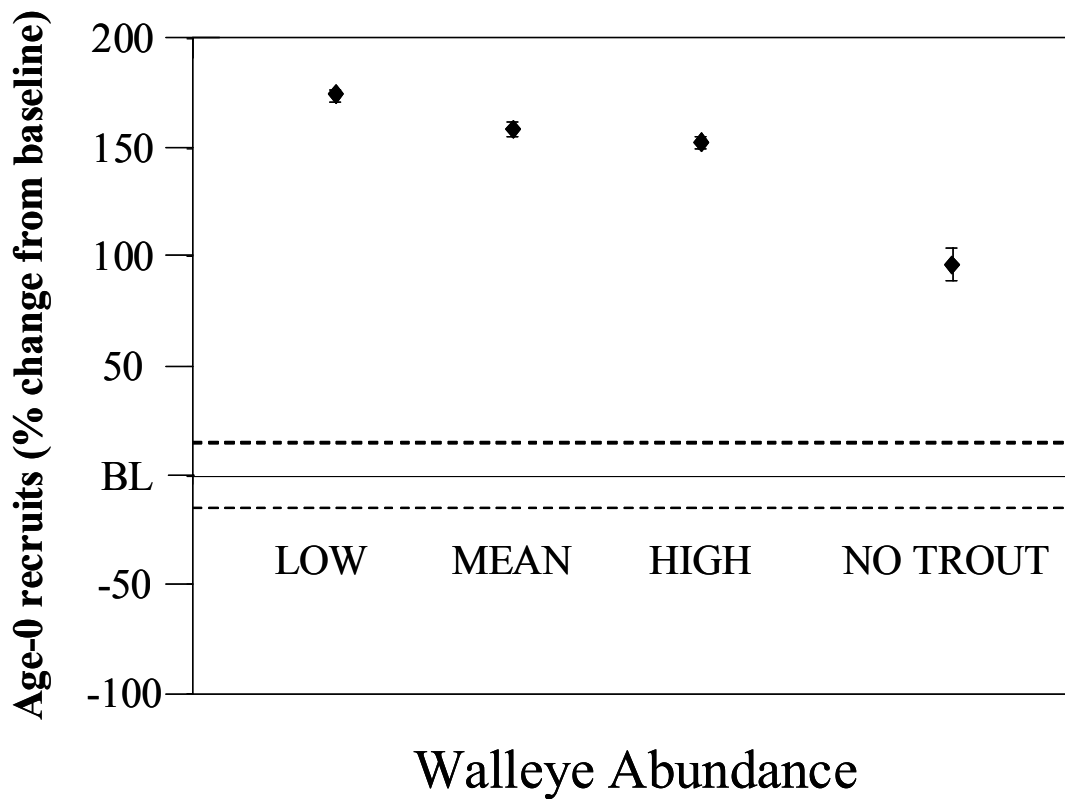


Figure 4.3. Percent change from baseline conditions in simulated recruitment of Chinook salmon with walleye predation and in the absence of piscivorous brown trout. Note the simulation “NO TROUT” represents a lack of hatchery rainbow trout as well. Error bars represent 95% confidence intervals around mean. Dashed lines represent 95% confidence intervals around the baseline estimate of recruitment.

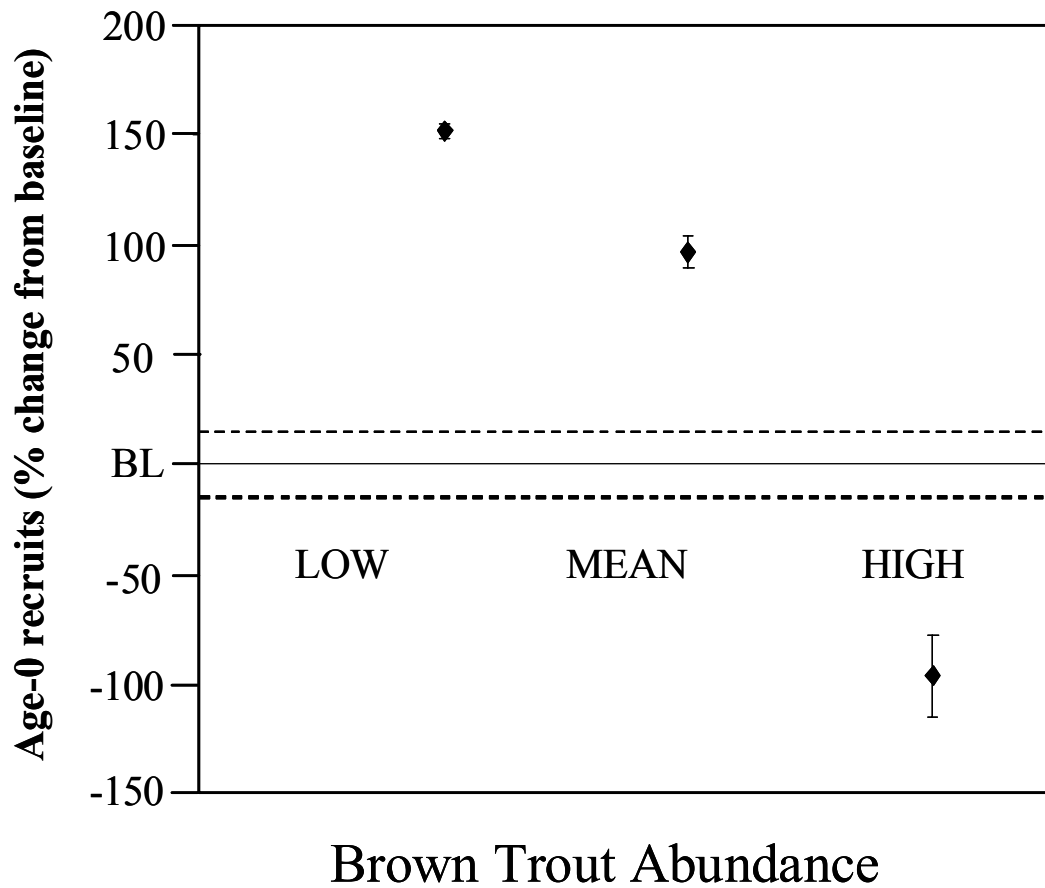


Figure 4.4. Percent change from baseline conditions in simulated recruitment of Chinook salmon with brown trout predation but in the absence of walleyes. Error bars represent 95% confidence intervals around mean. Dashed lines indicated 95% confidence intervals around the baseline estimate of recruitment.

Chinook salmon recruitment was inversely correlated with walleye abundance (Figure 4.5). Relative Chinook salmon recruitment was significantly lower than baseline in all instances of HIGH brown trout abundance (Figure 4.5) and Chinook salmon populations crashed whenever brown trout abundance was HIGH (Table 4.8). A lack of predation mortality from either walleyes or brown trout resulted in a significant (169%) increase in Chinook salmon recruitment compared to baseline. Simulated removal of all hatchery trout (walleyes present) led to a significant increase in Chinook recruitment while removal of Cyprinidae (hatchery trout and walleye present) resulted in recruitment that was significantly lower than baseline (Figure 4.5).

Simulated changes in alewife abundance affected Chinook growth and fecundity in Lake Michigan but did not significantly influence the long-term recruitment rates of Chinook salmon (Figure 4.6). Increases in environmental stochasticity to MODERATE levels significantly reduced Chinook salmon recruitment below baseline at LOW parr survival, did not significantly differ at MEAN survival and increased significantly at HIGH survival (Figure 4.6). The trend was similar when environmental stochasticity was again elevated to HIGH levels, although MEAN survival also resulted in a significantly lower recruitment compared to baseline.

Simulated changes in predator abundance (hence, parr survival) influenced the probability that the adult Chinook salmon population would decline to below one-third of its initial abundance (103,230 adults). When brown trout abundance was MEAN, the probability of such a decline was $\geq 69\%$ unless walleye abundance was LOW or absent (Table 4.8). At HIGH brown trout abundance, the probability of decline for Chinook was 100%, regardless of walleye abundance (Table 4.8). The probability of decline was also

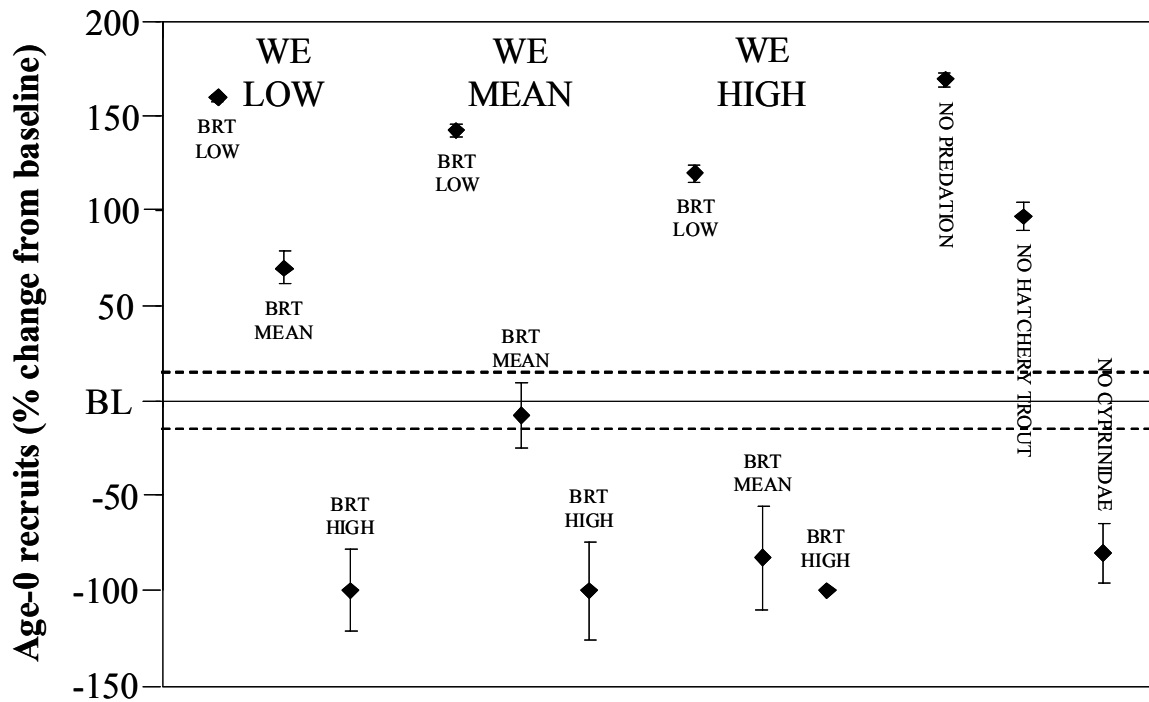


Figure 4.5. Percent change from baseline conditions in simulated recruitment of Chinook salmon with predation by variable abundances of walleyes (“WE”) and brown trout (“BRT”). Also included are simulations with 1) no predation mortality (NO WE, NO BRT), 2) no hatchery trout (no BRT, no rainbow trout), and 3) no Cyprinidae (WE MEAN, BRT MEAN). Error bars represent 95% confidence intervals around mean. Dashed lines indicate 95% confidence intervals around the baseline estimate of recruitment.

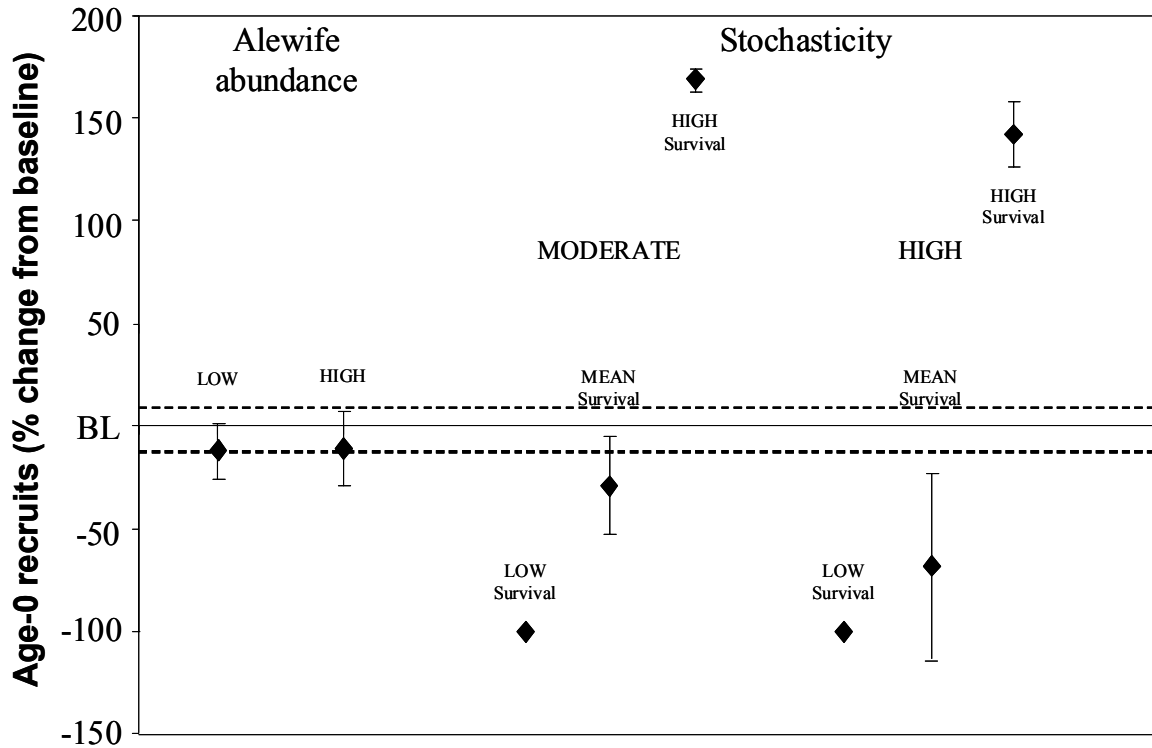


Figure 4.6. Simulated changes from baseline conditions of recruitment of Chinook salmon resulting from increased variation in Chinook survival and fecundity (stochasticity), and effects of variable adult salmon growth rate (alewife abundance) on salmon fecundity. Error bars represent 95% confidence intervals around mean. Dashed lines represent 95% confidence intervals around the baseline estimate of recruitment.

Table 4.8. Coefficients of variation for mean recruitment values over the last 10 years of each simulation and probability of decline for all simulations. “Crash” indicates that the population abundance fell below 1,000 individuals and the number in parentheses is the number of years it persisted.

Simulation	Coefficient of variation	Crash?	Probability of decline
WE ABSENT			
BRT LOW	0.009	no	0.02
BRT MEAN	0.013	no	0.02
BRT HIGH	na	yes (50)	1.00
WE LOW			
BRT ABSENT	0.004	no	0.02
BRT LOW	0.007	no	0.02
BRT MEAN	0.016	no	0.04
BRT HIGH	na	yes (50)	1.00
WE MEAN			
BRT ABSENT	0.013	no	0.02
BRT LOW	0.007	no	0.02
BRT HIGH	na	yes (36)	1.00
NO hatchery trout	0.007	no	0.02
WE HIGH			
BRT ABSENT	0.009	no	0.02
BRT LOW	0.014	no	0.98
BRT MEAN	0.119	no	1.00
WE MEAN, BRT MEAN	0.010	no	0.74
NO Cyprinidae	0.164	no	1.00
LOW alewife	0.060	no	0.74
HIGH alewife	0.064	no	0.76
Env. Stochasticity MODERATE	0.052	no	0.69
Env. Stochasticity HIGH	0.122	no	0.98
WE HIGH, BRT HIGH	na	yes (22)	0.02
Env. Stochasticity MODERATE	na	yes (23)	1.00
Env. Stochasticity HIGH	na	yes (25)	1.00
WE ABSENT, BRT ABSENT	0.007	no	0.02
Env. Stochasticity MODERATE	0.011	no	0.02
Env. Stochasticity HIGH	0.122	no	0.04

very high when environmental stochasticity was increased to MODERATE or HIGH levels but only if predator abundances were MEAN or HIGH (Table 4.8).

Variability in Chinook salmon recruitment increased with increasing levels of predator mortality on Chinook parr and with increasing variation around survival and fecundity rates. Increased environmental stochasticity generally yielded the highest variability in recruitment rates (Table 4.8; Figure 4.6). Removal of brown trout yielded the lowest variability in recruitment for individual predation scenarios (Table 4.8; Figure 4.5).

Discussion

The effects of predation during the parr stage appear to be highly influential on Chinook salmon recruitment, according to my analysis. At high predation levels, I observed a 100% decrease in Chinook salmon recruitment. On the other hand, several scenarios that included predator removals led to increased Chinook salmon recruitment by up to 174%. Although there appeared to be an interactive effect between brown trout and walleye on Chinook recruitment, brown trout were the dominant predator on Chinook parr. Hence, brown trout were responsible for the greatest changes (positive and negative) in Chinook salmon recruitment.

Predation on Chinook parr in the Muskegon River also had a large effect on the subsequent adult Chinook population. When brown trout were present at HIGH abundance, there was 100% probability that the adult Chinook population would drop below one-third of their initial abundance. Further, when HIGH brown trout abundance was combined with MEAN or HIGH walleye abundance, the Chinook population crashed. Environmental stochasticity also led to similar results, though only when

predator abundances were MEAN or HIGH. Some studies suggest that a recovering Chinook population is considered “healthy” when its abundance returns to one-third of its historical levels (Jager and Rose 2003). Hence, predation in the Muskegon River, especially by brown trout, has important consequences for the persistence of Chinook salmon in Lake Michigan. Walleye abundance did not have as big an influence as brown trout abundance on population persistence or recruitment of Chinook salmon.

The simulated effects of environmental stochasticity on Chinook salmon recruitment were generally negative unless predator abundance was LOW or ABSENT. While many of my simulations resulted in significant changes compared to baseline, simulations involving stochastic events produced the highest variability in recruitment (i.e., increase in error around mean). This supports data from Rutherford et al. (*in prep*) which indicate that Chinook salmon recruitment in the Muskegon River is much more variable (~ 10-fold) than was observed in Chapter 2 (~ 4-fold) over a similar time period. Therefore, environmental stochasticity may be more influential than I have modeled here, especially over shorter (< 10 years) durations. I modeled environmental stochasticity as an increase in standard deviations around mean values of adult fecundity and juvenile survival. At each time step in a simulation, RAMAS Stage chose parameter values from the stage matrix (fecundity, survival) and modified them (\pm) using a variance defined by the standard deviation matrix. The mean value of a particular variable, however, remained fairly constant throughout a simulation. Therefore, over longer durations, a population may recover from low densities potentially caused by stochastic events.

Results from RAMAS Stage were generally consistent with my previous foraging model (Chapter 3) although there were a few differences. For example, the foraging

model predicted that a cessation in hatchery trout (brown and rainbow trout combined) stocking efforts would lead to a 3.9% decrease in survival rates of Chinook salmon parr while RAMAS Stage predicted a substantial increase in recruitment. Such discrepancies between the forecasts of my foraging model and RAMAS Stage were likely due to density-dependence (Chapman 1962; Mason and Chapman 1965; Unwin 1986) which was incorporated in RAMAS Stage simulations but not in foraging model simulations. RAMAS Stage models density dependence explicitly as an interaction among juvenile Chinook salmon. Chinook salmon experience density dependence in the river and in the lake and these were expressed as changes in fecundity and survival in RAMAS Stage. In Lake Michigan, Chinook salmon growth and survival are dependent upon successful recruitment of alewife prey. In general, low alewife recruitment will lead to reduced size at age of Chinook salmon in subsequent years (Wesley 1996), though this is also dependent on the abundance of adult Chinook salmon. In river habitats, adult Chinook salmon compete for preferred spawning sites, while juveniles compete for access to preferred feeding and resting sites (Chapman 1966; Hearn 1987; Glova and Field-Dodgson 1995). Forecasts of my foraging model (Chapter 2) were dependent on the relative abundances of Chinook salmon and alternate prey species but were not dependent on intra-specific interactions. In the Muskegon River, high predation rates on Chinook parr can reduce the number of out-migrant smolts in a given year as my foraging model would predict. However, reduced resource competition may lead to increased parr size and improved smolt survival. Therefore, per capita recruitment into Lake Michigan may improve though it would take several years to detect. Hence, a short-term decline in

recruitment may actually lead to an increase in long-term recruitment as RAMAS Stage predicted.

While RAMAS Stage can be used to effectively model population dynamics of numerous species, I noticed obvious shortfalls of the program. For example, many important abiotic factors, such as river temperature and discharge, must be modeled implicitly. Because river temperature and discharge heavily influence predator feeding rates, changes in those factors were modeled as changes in parr survival. A spatially-explicit individual-based model (IBM) may be more adept at modeling population dynamics of Chinook salmon as it has the potential to adequately simulate processes in an ecosystem-level approach (Grimm et al. 2005). Compared to RAMAS Stage, an IBM can more easily incorporate mechanistic relationships between abiotic factors and individual feeding, growth, survival and fecundity (Jager et al. 1997; Godby et al. 2007). An IBM could also be used to explicitly model variable river discharge, which is positively correlated with Chinook recruitment (Seelbach 1985; Zafft 1992; Quinn 2005). Because an IBM can be parameterized to include habitat boxes representative of the Muskegon River, it could model density dependence between individual Chinook parr more effectively than RAMAS Stage. Therefore, an IBM may provide indices that may be more useful towards forecasting the impact of management manipulations on long term population dynamics. RAMAS Stage, on the other hand, is a useful tool for population dynamics modeling because of its relative simplicity. This model is more easily parameterized than an IBM and is accessible to a wider user base. It relies on easily obtainable demographic information and uses a minimal number of intensive

calculations which allows for quick simulations. Further, it gives researchers the ability to model environmental and demographic stochasticity and density dependence.

Several assumptions were necessary to use RAMAS Stage to represent the fish community and interspecific interactions in the Muskegon River. I assumed that piscivore feeding behavior was constant throughout 50 years of simulations. This further assumed that the results of Chapter 3 were not anomalous and the foraging model adequately described feeding behavior of walleyes and brown trout. Previous estimates of predation mortality (Chapter 2) were likely conservative as there may have been additional predation mortality in areas I couldn't sample effectively (i.e., deep water habitats). Further, I only used estimates of predation mortality to calculate survival of Chinook salmon for my simulations. Although I did not quantify it, Chinook salmon likely experienced additional stream mortality due to sources other than predation such as disease (Fitzsimons et al. 2007), which implies that actual mortality rates may be higher still. While my assumption that Chinook parr have 100% survival without predation may not be realistic, I was able to use empirical estimates of predation mortality to generate worthwhile simulations to investigate the relative influence of predation on recruitment dynamics. Further research should strive to examine and quantify all sources of stream mortality.

Other assumptions of fecundity relationships and type of density dependence incorporated in the RAMAS model were likely not as critical as those listed above. I used length-fecundity estimates for Pacific Coast populations of Chinook salmon to estimate fecundity of salmon in Lake Michigan. Relative fecundities of Lake Michigan salmon may be higher or lower. Finally, I used the ceiling type of density dependence in

my simulations which did not allow us to specify a maximum population growth rate (R_{max}). Still, this type of density dependence has been used to model Coho salmon, a closely related species (Bradford et al. 2000). Because of the many density dependent factors influencing the riverine life stages of Chinook salmon (i.e., redd competition in adults, feeding and resting site competition in juveniles), not allowing a population to exceed an arbitrary carrying capacity does not seem an implausible option. Further, the ceiling type of density dependence does not necessarily allow a population at low abundance to recover as the Beverton-Holt (compensatory) and Ricker (over-compensatory) types would. For example, a scenario simulating persistently low parr survival ($S = 0.06$) and using the ceiling type density dependence will lead to a population crash. The Beverton-Holt and Ricker types of density dependence, however, would allow a population to persist with the same parr survival rate.

Management Implications for Lake Michigan

This simple model to describe the effect of species interactions in the Muskegon River could serve as a tool for fishery managers to develop and evaluate stocking scenarios (Cox and Walters 2002) for sport fisheries in Great Lakes and coastal ocean tributaries that contain important salmonid nursery habitats. A goal of the Fish Community Objectives for Lake Michigan (Eshenroder et al. 1995) is to maintain Chinook salmon at stable densities and balance predator and prey communities (Claramunt et al. 2009). One step towards realizing this goal is to minimize variability observed in wild Chinook salmon recruitment. Aside from stocking, Claramunt et al. (2009) proposed altering habitat conditions to influence natural recruitment as a management tool to meet objectives. I argue that habitat can be defined not only by physical structure but also by

the fish community present in a system. Given the ability of brown trout to influence variability in Chinook salmon survival and recruitment, this seems an appropriate argument. By manipulating the abundance of an important predator, I have shown that management actions to reduce stocking efforts can significantly improve long-term recruitment and reduce recruitment variability of Chinook salmon in important tributaries. Based on my simulations, removal of walleyes from the Muskegon River does not appear to be warranted, which is good news for managers since walleyes are highly sought after by anglers in this system (Chapter 2).

The Muskegon River was an ideal system for this analysis as fishery managers essentially have total control of predator abundance. Hence, through stocking efforts, walleye and brown trout predation effects on Chinook salmon parr can be controlled as well. Theoretically, long term recruitment of Chinook salmon can also be controlled through manipulation of important predators. Similar assertions have been made in other studies to promote persistence of Great Lakes piscivores (e.g., Kitchell and Crowder 1986; Kitchell et al. 2000). Managers could apply this model to other systems to determine the population consequences of stream piscivores on long-term Chinook salmon reproduction. Although my modeling effort was simple, it is the first such analysis of a Lake Michigan tributary and may provide the first step towards implementing such actions.

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Chapter V

Implications of Fishery Management actions on Chinook Salmon Survival and Recruitment in the Muskegon River, Michigan: A Synthesis

An improved understanding of ecosystem-level processes is important for understanding species' population dynamics and formulating fisheries management recommendations. In this dissertation, I have described species interactions and their ramifications for Chinook salmon recruitment and population dynamics across various temporal and spatial scales. Fine temporal and spatial scale patterns in growth and survival of Chinook salmon parr were discernable through mean daily rations of piscivores throughout the Muskegon River Estuary System. Detailed analyses of piscivore feeding behavior supported development of predator foraging models that were used to evaluate consequences of management scenarios for population dynamics and recruitment of Chinook salmon. Hence, the recommendations I have set forth are based on robust patterns and may be applicable in multiple regions.

Based on the results of the three research chapters (2 – 4) of this dissertation, I concluded that in some years, environmental processes (i.e., river temperature and discharge) may not explain typical levels of recruitment variability observed in Muskegon River Chinook salmon. Departures from mean river temperature and discharge did not correspond with a noticeable trend in survival of Chinook salmon parr

(or recruitment). On the contrary, extensive analysis of piscivore diets suggested that variable piscivory, especially from walleyes and brown trout, did explain recruitment variability in Chinook salmon. Walleyes and brown trout preyed upon Chinook salmon parr more than any other piscivore in the Muskegon River. Brown trout were much more numerous than walleyes and, although much smaller, consumed a much greater proportion of available Chinook salmon parr. Their diet patterns, however, suggested that brown trout piscivory (on Chinook salmon parr) was regulated by prey size. Conversely, walleyes typically consumed much larger prey; brown trout and rainbow trout composed a majority of walleye diets for the duration of all sampling seasons. Although walleyes did consume Chinook salmon parr, there was no consistent trend between years. The availability of alternate walleye forage and the temporal overlap between Chinook salmon parr and brown trout were correlated with survival of Chinook salmon parr.

Predator feeding behavior and a foraging model helped inform management recommendations in the Muskegon River. Early in the spring (especially in April), brown trout positively selected Chinook salmon parr as their major prey source but in later months brown trout selection waned. In April and May, brown trout consumed Chinook salmon parr that were smaller than the average sized parr in the river. However, brown trout did not consume Chinook salmon parr once they reached a maximum prey/predator length ratio of 26% even though this was within the constraints of a brown trout gape limit (~ 40% TL; Damsgård 1995). Daily rations of brown trout were composed mostly of Chinook salmon parr in April, balanced between parr and stream invertebrates in May, and entirely stream invertebrates by June. A multi-species

functional response model suggested that brown trout were not satiated by the abundances of Chinook salmon parr observed in the Muskegon River. This result implies that if piscivorous brown trout are stocked early in the spring (i.e., April) when Chinook salmon parr are small, brown trout are capable of consuming a significant fraction of available Chinook salmon parr in a given year.

Like brown trout, walleyes also consumed prey fish that were smaller-than-average. Walleyes selected for rainbow trout prey during several months of the study but showed the opposite behavior toward brown trout prey. I hypothesized that differences in brown trout and rainbow trout foraging behavior placed the prey species in different parts of the river and resulted in differential spatial overlap with walleye. Chinook salmon parr were negatively selected by walleyes in two entire seasons (2006, 2007). Schooling behavior of Chinook parr (Petersen and Gadomski 1994; Petersen and DeAngelis 2000) may account for this phenomenon but may also explain why some walleyes consumed upwards of 50 Chinook parr in one meal. Overall differences in spatial distribution between walleyes and prey may also explain the lack of small fishes such as Chinook salmon in their diets. Chinook parr were found in very shallow water, while walleyes were found in the thalweg, plunge pools and deep corners of the river. Further, walleyes forage at low light while juvenile salmon tend to decrease their movements during darkness (Ledgerwood et al. 1991), which may lower encounters with walleyes (Petersen and Gadomski 1994). Regardless, cessation of brown trout stocking efforts was the most promising management action for increasing survival of juvenile Chinook salmon.

The foraging relationships and empirical studies provided information to parameterize a stage-based model to forecast the consequences of fish interactions on

long-term population dynamics of Chinook salmon in the Muskegon River. Many of the stage-based modeling simulations substantiated the short-term forecasts of the functional response model. I found that walleye removals were not effective towards increasing Chinook recruitment. On the other hand, simulations that incorporated removal of brown trout resulted in a significant increase in Chinook salmon recruitment and reduced the likelihood that the adult population would fall below “healthy” abundance levels (e.g., Jager and Rose 2003). Stochastic events were an added element of the stage-based modeling approach and led to the greatest amounts of variability in recruitment though they only positively influenced Chinook recruitment when parr survival was very high. Still, variable brown trout abundance led to large variations (positive and negative) in Chinook salmon recruitment and their effects were generally independent of walleye abundance. Hence, implementation of my management recommendations to halt stocking of brown trout would yield immediate benefits for Chinook salmon survival and would also increase long-term recruitment of Chinook salmon.

Management Recommendations

Whether stocked or wild produced, Chinook salmon parr face similar challenges that lead to variable recruitment. In Lake Huron’s Thunder Bay, stocked salmonids simply provide forage for walleye, lake trout and cormorants and do not typically reach adulthood (Johnson et al. 2007). However, if managers employ an appropriate stocking window, predation mortality can be minimized. In Thunder Bay, walleyes preferentially consume alewife over Chinook salmon smolts. When Chinook smolts were released and alternate forage was abundant (i.e., May), smolt survival increased (Johnson et al. 2007). In the Muskegon River, the presence of alternate forage for walleyes led to reduced

predation mortality on Chinook parr. Despite the spatial differences, my dissertation research also showed that Chinook parr would benefit from a stocking window. Brown trout only imposed high predation rates on Chinook salmon parr in the early spring when they were most vulnerable. Brown trout stocking should only occur after parr have reached a size (TL > 50 mm) to outgrow predation vulnerability from brown trout. This would substantially improve parr survival and minimize variability observed in wild Chinook salmon recruitment, a goal of the Lake Michigan Fish Community Objectives (Eshenroder 1995).

Predation and other species interactions can be controlled directly and indirectly through manipulation of predatory fishes via stocking efforts and fishing regulations (e.g., Krueger and Hrabik 2005). While I did not focus on fishing regulations in my dissertation, I have shown the effects of predation via stocked brown trout and walleyes and I base the following recommendations on that information.

Brown trout appear to have significant effects on Chinook salmon recruitment and population dynamics through predation on parr and these effects are realized across multiple spatial and temporal scales. Therefore, I recommend changes in the timing or numbers of brown trout stocked in the Muskegon River and other Lake Michigan tributaries that rely on wild Chinook production. While brown trout are not highly sought-after by Muskegon River anglers (Tracy Kolb Michigan Department of Natural Resources personal communication), they may be targeted in other systems. In this instance, I recommend that managers utilize a stocking window where brown trout are stocked in mid to late May and over the course of several weeks. For example, stocking 32,000 brown trout (165 mm TL) in four efforts beginning in mid May would probably

result in low predation mortality on Chinook salmon parr (via brown trout). This management strategy would also lead to improved Chinook salmon recruitment and reduced recruitment variability.

Other considerations

In this dissertation, I proposed that survival of juvenile Chinook salmon could be an important predictor for short (≤ 10 years) and long-term (> 10 years) population dynamics in the Muskegon River. This assertion appears to be supported by empirical data (short term) and by some modeling scenarios where brown trout were either very low in abundance or altogether absent (long term). There are, however, multiple factors that could influence Chinook salmon population dynamics over multiple temporal and spatial scales.

While juvenile survival depends heavily on riverine processes, the majority of the Chinook life cycle occurs in pelagic water (Lake Michigan proper or the open ocean) and there are a number of factors therein that could represent a potential bottleneck for Chinook salmon survival and persistence. The pelagic environment can have a dramatic influence on size-at-age and age-at-maturity of Chinook salmon (Wells et al. 2007). Decreased size-at-age could lead to delayed maturation (Healey 1991) and an increased duration where individuals are vulnerable to predation. Marine survival of Columbia River stocks, for example, is thought to be predation-driven and a large proportion of predation mortality occurs in estuary habitats (Emmett and Sampson 2007). Middlemas et al. (2009) showed that the highest levels of predation mortality on anadromous brown trout also occurred in estuaries. This is likely the case in the Great Lakes though I was unable to determine estuarine predation on Chinook parr in the Muskegon River Estuary

System. Still, it appears that in all instances, predation mortality would be considerably reduced provided that alternate forage for Chinook predators was abundant (e.g., Johnson et al. 2007).

Oceanographic conditions likely have widespread impacts on salmonid stocks in multiple regions and may have caused the observed decline in a number of salmon stocks in the Pacific Northwest (Mantua et al. 1997). Wells et al. (2007) found that the 1982 – 1983 El Niño Southern Oscillation (ENSO) event led to a 30% decrease in fecundity of Coho salmon (*O. kisutch*) in Oregon. Further, salmon productivity in the Pacific Northwest appears to be strongly correlated with the Pacific Decadal Oscillation (PDO); salmon productivity was generally lower than expected when PDO values were negative (Levin 2003). Responses to ocean/climate change, however, were not the same among all salmonid stocks.

Unfortunately, little is known about the connection between oceanographic conditions and pelagic survival of salmon (Friedland 1998; Pyper et al. 2005) in the Great Lakes. Like the Pacific Ocean (perhaps to a much lesser extent), the Great Lakes are affected by PDO and ENSO through changes in weather patterns that lead to changes in precipitation, stratification timing, ice cover and duration of ice cover (Rodionov and Assel 2003; Winder and Schindler 2004). These factors strongly influence primary productivity of lake and river systems in the Great Lakes region. Researchers and managers must, therefore, carefully re-evaluate the ability of the Lake Michigan food web to distribute nutrients throughout the fish and invertebrate communities and sustain Chinook salmon populations. Indeed, realizing the Fish Community Objectives set forth

for Chinook salmon may be more difficult than deciding whether or not to stock hatchery-reared fish in tributaries.

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