EVALUATING THE EFFECTS OF RAINBOW SMELT ON NATIVE PISCIVORES IN FRESHWATER SYSTEMS WITH A SPECIAL FOCUS ON WALLEYE RECRUITMENT AND LARVAL BIOENERGETICS

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ABSTRACT

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Since the early 1900’s rainbow smelt (*Osmerus mordax*)have been introduced into many new freshwater inland systems outside of its native range. In freshwater systems the interaction between rainbow smelt and native piscivores differs from species to species. In some cases predation or competitive interactions between juvenile piscivores and adult rainbow smelt can limit recruitment success of piscivores. In other cases, rainbow smelt have no such impacts on piscivores and only serve as a forage fish. In a literature review, I explored rainbow smelt interactions with three different piscivore species, Atlantic salmon (*Salmo salar*), lake trout (*salvelinus namaycush*) and walleye (*Sander vitreus*). Differences in larval rearing strategies were identified as the most important factor in determining the nature of effects of rainbow smelt. In particular, larval walleye experience high levels of mortality after rainbow smelt establishment. A foraging-based bioenergetic model was created to determine if the zooplankton community that results from rainbow smelt establishment creates an “energetic bottleneck” for larval walleye. I assessed larval walleye densities and pelagic zooplankton communities in four lakes in Northern Wisconsin with differing populations of rainbow smelt. Results indicate that rainbow smelt do not prey on larval walleye but an energetic bottleneck may exist at low zooplankton biomasses.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Invasive species are a leading cause of biodiversity declines in the world (Sala et al. 2000, Wilcove et al. 2007). In addition to homogenizing biodiversity, invasive species also cause significant economic costs. Pimentel et al. (2005) estimated that invasive species in the United States cause approximately 120 billion dollars in damages each year, with invasive fish species alone accounting for 5.4 billion dollars in damages. Freshwater systems are particularly vulnerable to these biologic and economic impacts due to their high levels of endemism (Richter et al. 2007). A critical step in slowing and preventing invasive species from their establishing in new habitats is to increase our knowledge about invasive species and their impacts on ecosystems (Vander Zanden and Olden 2008). The rainbow smelt (*Osmerus mordax*) is one invasive species that poses a threat to many freshwater systems across North America.

The impacts of invasive rainbow smelt extend to many native fish species. Rainbow smelt have caused declines in both cisco and lake white fish due to predation on their larvae (Loftus and Hulsman 1986, Evans and Loftus 1987, Hrabik et al. 1998). Yellow perch numbers were driven to almost nonexistent levels in Crystal Lake, Wisconsin due to competitive interactions with rainbow smelt (Hrabik et al. 2001). Recruitment declines have also been observed in burbot (*Lota lota*) and alewife (*Alosa pseudoharengus*) due to rainbow smelt introductions (Kircheis and Stanley 1981, Evans and Loftus 1987). Rainbow smelt also cannibalize their own young, a process that drives cyclical fluctuations in abundance in both large and small systems (Lantry and Stewart 2000, Roth et al. 2010). These radical swings in abundance can have negative consequences for the piscivores that depend on consistent forage base (Stewart et al. 1981, Gorman 2007). Outside of their native range, rainbow smelt introductions have had consistently negative repercussions on native fish communities.

This study focuses on the current status of rainbow smelt and their interactions with native piscivores, specifically Atlantic salmon (*Salmo salar*), lake trout (*Salvelinus namaycush*), and walleye (*Sander vitreus*) in freshwater systems. Rainbow smelt are consumed by the adults of these predators across a wide variety of freshwater habitats (Nellbring 1989).Despite a predatory relationship with rainbow smelt, both lake trout and walleye populations experience recruitment declines after the establishment of rainbow smelt. However, recruitment does not decline in landlocked Atlantic salmon populations that overlap with rainbow smelt populations (Kirn and LaBar 1996, Boucher 2004, Rooney and Paterson 2009). Juxtaposing the effects of rainbow smelt on different piscivores across an array of habitats will shed light on the biological or environmental cues responsible for these different responses. In particular, I'll examine life history strategies of each of these piscivore species and how it affects their interactions with rainbow smelt. Invasive rainbow smelt will continue to expand their range and alter native fish communities for the foreseeable future, making well informed and effective management policies a top priority (Mercado-Silva et al. 2006). A better understanding of how rainbow smelt impact these species will help biologists to better manage these economically and culturally important species.

RAINBOW SMELT GEOGRAPHIC DISTRIBUTION

Rainbow smelt are an anadromous species native to the coastal regions of the North Atlantic and North Pacific (Scott and Crossman 1973, Buckley 1989). On the Atlantic coast they can be found from Nova Scotia to New Jersey, while on the Pacific coast they can be found from Northern Alaska to Southern British Columbia (Rupp and Redmond 1966, Fuller et al. 1999). Despite their anadromous life history, they do occur natively in freshwater systems. As such, rainbow smelt comprise an important part of the native pelagic fish community in numerous lakes in Southern Maine and Lake Champlain (Rupp 1959, Kirn and LaBar 1996, Pellerin 2005). They are also native to lakes as far inland as Eastern Ontario (Lakes Muskrat, Dore, and Golden) and possibly even Lake Timiskaming (Evans and Waring 1987)(Figure 1). It should be noted that native population of rainbow smelt this far west is uncommon. These populations are likely derived from remnants of populations within the ancient Champlain Sea (present day St. Lawrence drainage) which extended into present day Eastern Ontario approximately 11,000 years bp (Mandrak and Crossman 1992). Despite being native to a few freshwater systems, rainbow smelt are non-native to most freshwater systems they currently occupy.

Rainbow smelt now occupy many habitats outside of their historical native range, including the Great Lakes. They were first introduced outside of the St. Lawrence drainage into Crystal Lake, Michigan to serve as a forage fish for a stocked population of landlocked Atlantic salmon (Creaser 1929, Van Oosten 1937). Due to Crystal Lake's proximity and connectivity to Lake Michigan, by 1925 rainbow smelt found their way into Lake Michigan. In the late 1920's, rainbow smelt were stocked in New York's Finger Lakes, from which they quickly invaded Lake Ontario (Bergstedt 1983). By 1936, rainbow smelt were collected in all five Great Lakes (Van Oosten 1937, Dymond 1944). Since becoming established in these systems, rainbow smelt have grown to play an important role as a forage fish for salmonids that are fished both recreationally and commercially (Argyle 1982, Rand and Stewart 1998b, a).

In addition to the Great Lakes and areas of the Saint Lawrence drainage, rainbow smelt were also introduced to the Missouri and Mississippi river systems. Rainbow smelt in these large river systems are most often confined to reservoir habitats due to their requirement for cold, oxygenated water. Rainbow smelt were stocked in Lake Sakakwea in North Dakota in 1971 as a forage fish for a stocked population of white bass (*Morone chrysops*) (Owen et al. 1981, Mayden et al. 1987). There is evidence that these rainbow smelt migrated upstream and established a population in Lake Fort Peck, Montana as well (Gould 1981). Rainbow smelt were accidently introduced to Lake Oahe (South Dakota) in 1974, where they quickly established a naturalized population. Within four years rainbow smelt comprised the largest proportion of fish biomass in the reservoir (Owen et al. 1981). Rainbow smelt are found commonly throughout the Missouri River between Lake Oahe and downstream to the confluence of the Missouri River with the Mississippi River. All populations below Lake Oahe are the direct result of intentional stocking events that took place in several reservoir systems within the river (Harlan et al. 1987, Mayden et al. 1987, Young et al. 1997). From the confluence with the Missouri River, rainbow smelt have been found in the Mississippi River as far south as Louisiana. Although uncommon this far south, juvenile rainbow smelt have been collected in St. Francisville, Louisiana, which indicates natural reproduction has occurred in the region (Burr and Mayden 1980, Suttkus and Conner 1980, Mayden et al. 1987, Robinson and Buchanan 1988).

Rainbow smelt have been introduced into many smaller inland systems across the eastern, central and western portions of North America. Rainbow smelt were stocked during the 19th century as forage fish for populations of landlocked Atlantic salmon across the Northeastern United States (Carlson and Daniels 2008). These stocking locations include all the Finger Lakes as well as several lakes within the Adirondack reserve(Werner 1980, Bergstedt 1983, Carlson and Daniels 2008). Within Maine, rainbow smelt are native to many inland lakes in the Southern coastal region of the state. Currently, rainbow smelt occupy over 550 Maine lakes where they serve almost exclusively as a forage fish for landlocked Atlantic salmon (Fuller et al. 1999, Pellerin 2005). Determining how many and which lakes rainbow smelt are native to in Maine is impossible due to widespread stocking, both documented and undocumented, over the last 100 years. In the Great Lakes region, rainbow smelt have secondarily invaded many inland lakes in the region (Evans and Loftus 1987, Mercado-Silva et al. 2006). Rainbow smelt are now found in 27 inland lakes in Wisconsin, mostly concentrated in the northern third of the state(Mercado-Silva et al. 2006, Mercado-Silva et al. 2007). Michigan also has a few inland lakes that contain rainbow smelt populations scattered throughout the state(Burbidge 1969, Laarman 1976, MIDNR 2011). Since the 1960's rainbow smelt have also become distributed across numerous inland lakes within Minnesota, Ontario and Manitoba. These introductions were mostly accidental although many introductions are thought to be intentional but done without the consent of management agencies (MacCrimmon et al. 1983, Hassinger and Close 1984, Evans and Loftus 1987, Campbell et al. 1991, Franzin et al. 1994, Remnant et al. 1997). In the western United States, rainbow smelt were introduced into the Horsetooth reservoir in

Colorado as an attempt to bolster the forage base for stocked piscivorous game fish (Jones et al. 1994, Johnson and Goettl Jr 1999).

RAINBOW SMELT DISPERSAL MECHANISMS

Rainbow smelt have spread into all the lakes and rivers listed above through human introductions and subsequent dispersal. The most common vector for rainbow smelt introductions continues to be human activities (Vander Zanden and Olden 2008). Intentional introductions of rainbow smelt are almost exclusively for the purpose of providing forage fish for piscivorous sport fish (Mercado-Silva et al. 2006, Rooney and Paterson 2009). Unintentional introductions are generally the result of one of two actions. One possibility is the transfer of smelt during angling activities. Rainbow smelt may be released as unused baitfish (Halliwell et al. 2001) or fertilized eggs may be transferred while cleaning harvested rainbow smelt (Evans and Loftus 1987). As a second possibility, fertilized eggs may also be released into new waters if they become attached to macrophytes or rocks that are transported by boaters (Kircheis and Stanley 1981). Lake connectivity can also be an important factor in the dispersal of rainbow smelt. Smelt larvae are capable of drifting several kilometers after hatching and can drift into new lakes via outlet streams (Densen and Vijverberg 1982, Næsje et al. 1987). They may also disperse into new lakes during their upstream spawning runs in the spring. However, this type of dispersal is dependent on low stream gradients and flows as well as the stream distance between lakes (Hrabik and Magnuson 1999).

RAINBOW SMELT LIFE HISTORY

Like other members of the *Osmeridae* family, rainbow smelt exhibit a strong preference for coldwater (Scott and Crossman 1973). Rainbow smelt have a eurythermal life history, meaning they prefer different temperatures at different stages in their life. As adults in freshwater systems they occupy deep pelagic waters. During the summer months they're restricted to depths near the thermocline (Halliwell et al. 2001). This cold water preference restricts rainbow smelt from occupying many shallow lakes or eutrophic lakes that experience hypolimnetic anoxia (Mercado-Silva et al. 2006).In contrast to adults, yearling rainbow smelt occupy the mid-level depths of pelagic zone and young-of-year (YOY) rainbow smelt occupy warmer littoral waters (MacCallum and Regier 1970, Brandt et al. 1980, Lantry and Stewart 1993). The physical separation of the different life stages of rainbow smelt minimizes intraspecific competition, resulting in a partitioning of food resources(Evans and Loftus 1987).

The diets of rainbow smelt vary considerably among life stages due to their opportunistic feeding habits. YOY smelt consume small plankton items such as copepod nauplii, rotifers and diatoms due to gape limitation(Evans and Loftus 1987, Næsje et al. 1987).As yearlings (age 1+), rainbow smelt consume primarily crustacean prey, however they will also cannibalize YOY rainbow smelt when strong YOY year-classes occur (Lantry and Stewart 2000, Stetter et al. 2004, Gorman 2007). Adult rainbow smelt feed primarily on zooplankton, other crustaceans and insects(Gordon 1961, Burbidge 1969, Foltz and Norden 1977). As visual feeders, they show an active preference for large bodied cladoceran species (eg. *Daphnia*) (Gliwicz et al. 2004, Johnson et al. 2004) and they will consume larger items such as *Mysis relicta, Leptodora kindtii*, and Dipteran larvae if present(Urban and Brandt 1993, Johnson et al. 2004). Fish do not begin to appear in rainbow smelt diets until they reach a length between 130 mm – 170 mm (Maccrimmon and Pugsley 1979, Evans and Loftus 1987). Fish gradually comprise larger proportions of rainbow smelt diets as size increases (Evans and Loftus 1987). Fish that are consumed are usually YOY fish as well as smaller adult species such as cyprinids. Fishes that are known to be consumed by rainbow smelt include: lake whitefish (*Coregonus clupeaformis*) (Loftus and Hulsman 1986), emerald shiners (*Notropis atherinoides*) (Maccrimmon and Pugsley 1979), cisco (*Coregonus artedii*) (Selgeby et al. 1978, Selgeby et al. 1994, Hrabik et al. 1998), slimy sculpin (*Cottus cognatus*) (Brandt and Madon 1986) and lake trout (Riley and Marsden 2009).

Rainbow smelt begin spawning early in the spring soon after ice off and sometimes before ice off (Pugsley 1976, Lischka and Magnuson 2006). Sexual maturity is typically reached at lengths less than 150mm, which generally corresponds to age-2 and age-3 fish (Kircheis and Stanley 1981). There are two distinct spawning strategies for landlocked rainbow smelt. The preferred strategy is to make spawning runs up inlet streams where eggs are dispersed onto cobble and rock substrate (Hoover 1936). The second strategy occurs if no inlet stream exists for the water body the rainbow smelt inhabit. Under these circumstances they will instead move inshore (depths of < 2m) to spawn over cobble substrate (Lischka and Magnuson 2006). In either case, spawning occurs immediately after ice-off in waters that freeze; however spawning runs underneath the ice are not uncommon (MacCrimmon et al. 1983, Curry et al. 2004). After spawning the rainbow smelt return to the pelagic area of the lake. Post-spawning die offs have been reported in Lake Erie but the vast majority of populations are iteroparous (Scott and Crossman 1973). Hatch time for the eggs is temperature-dependent and can take two to four weeks. After hatching rainbow smelt larvae drift downstream into the lake and occupy the warmer epilimnetic waters as they begin feeding (Nellbring 1989, Rooney and Paterson 2009).

RAINBOW SMELT INTERACTIONS WITH NATIVE PISCIVORES

ATLANTIC SALMON

One species that rainbow smelt commonly interact with is Atlantic salmon (*Salmo salar*), which are found throughout northeastern North America. Atlantic salmon area cold-water fish and are members of the *Salmonidae* family. Although they are primarily an anadromous species of the North Atlantic, they are also native to landlocked freshwater systems throughout coastal regions of Maine, New Brunswick, Nova Scotia and even Lake Ontario(Scott and Crossman 1973, Smith 1995). By the 1890's, however, the Lake Ontario population had been extirpated due to over harvesting and spawning habitat degradation(Scott and Crossman 1973, Boucher and Warner 2006). Rainbow smelt and Atlantic salmon are both native to these areas and commonly coexist within this region(Kircheis and Stanley 1981, Pientka and Parrish 2002).

During the last 100 years freshwater stocking efforts have increased the Atlantic salmons' range to include lakes in Northern Maine, New Hampshire, Vermont, New York and several of the Great Lakes (Halliwell et al. 2001). The widespread stocking of Atlantic salmon into new systems has been due to its popularity as a sport fish (Halliwell et al. 2001).In Maine, Atlantic salmon are the most sought after cold-water inland fish by anglers (Boucher 2004). Rainbow smelt are often stocked in conjunction with Atlantic salmon because Atlantic salmon's strong preference for rainbow smelt as a forage fish and their similar coldwater habitat requirements (Kircheis and Stanley 1981, Pientka and Parrish 2002).

The predator-prey relationship between landlocked Atlantic salmon and rainbow smelt is relatively well understood. Wherever the two species are found together, rainbow smelt are the preferred forage fish for adult Atlantic salmon (Table 1)(Stillwell and Stanley 1883). The preference for rainbow smelt is so strong by Atlantic salmon that their growth rates and body conditions are tightly correlated with the size of rainbow smelt populations (Kirn and LaBar 1996, Boucher 2004). For example, in Schoodic Lake, Maine, declines in smelt biomass were followed by declines in Atlantic salmon growth rates (Havey 1973). Such tight relationships are not surprising given that in some instances Atlantic salmon feed almost exclusively on rainbow smelt (Kendall 1935, Cooper and Fuller 1945, Fuller and Cooper 1946, Boucher and Warner 2006). The role of rainbow smelt as a forage fish for Atlantic salmon is such that the primary concern for inland Atlantic salmon management in Maine is the maintenance of rainbow smelt populations (Boucher 2004). Rainbow smelt however, do not adversely affect Atlantic salmon populations (Havey 1973, Evans and Loftus 1987, Rooney and Paterson 2009). The interactions between rainbow smelt and Atlantic salmon appear to be strictly predator-prey relationships.

One likely reason for the lack of any negative effects by rainbow smelt on Atlantic salmon is the physical separation of the two species during the juvenile stage of the Atlantic salmon. During this period of the Atlantic salmon life cycle, rainbow smelt could prey on or compete with young salmon. However, Atlantic salmon juveniles usually spend one to two years in connecting streams until they smolt and return to the lake (Boucher 2004). Upon returning to the lake, Atlantic salmon have reached a size (approx. 200 mm) no longer vulnerable to the negative effects of rainbow smelt (Klemetsen et al. 2003).It should be noted there are populations of landlocked Atlantic salmon whose parr are reared within the lake rather than in the stream environment. This variation in life history is rare and is constrained to a few isolated systems (Marschall et al. 1998, Klemetsen et al. 2003, Verspoor and Cole 2005). The lack of spatial overlap between rainbow smelt and juvenile Atlantic salmon prevents rainbow smelt from having any predatory or competitive interaction with the YOY Atlantic salmon. The relationship between these two natively coexisting species appears to be strictly a predator-prey relationship.

LAKE TROUT

Unlike Atlantic salmon, it's unknown whether lake trout and rainbow smelt occur together natively. Lake trout are a common species native to many lakes across northern North America (Scott and Crossman 1973, Lee et al. 1980). The expansion of rainbow smelts' range as a result of widespread stocking and a lack of documentation have made deciphering to what extent these two species natively coexisted unlikely. In one exception, Riley and Marsden (2009) suggest that both lake trout and rainbow smelt may be native to Lake Champlain. However, the most common mechanism that causes rainbow smelt and lake trout to overlap is the introduction of rainbow smelt into the system. For example, rainbow smelt were not present in any of Maine's lake trout waters but due to stocking, rainbow smelt now occupy 93% of those lakes (Johnson 2001). Due to their limited native presence in inland systems, rainbow smelt should be considered an exotic species for most lake trout populations.

Similar to Atlantic salmon, adult lake trout are cold-water piscivores that will readily consume rainbow smelt. Rainbow smelt and lake trout both prefer the colder temperatures of the deep pelagic zone in lakes, which creates substantial habitat overlap and opportunities for predation (Stewart et al. 1981, Buckley 1989, Kirn and LaBar 1996). Lake trout diets become dominated by rainbow smelt following their introduction. In both Lake Superior and Lake Champlain, rainbow smelt comprised over 60% of lake trout diets (LaBar 1993, Kirn and LaBar 1996, Ray et al. 2007). In Maine lakes, lake trout diets are almost exclusively rainbow smelt (Johnson 2001). Lake trout diets were similarly dominated by rainbow smelt after their introduction in West Bearskin Lake and Devilfish Lake, Minnesota (Hassinger and Close 1984). In contrast to Atlantic salmon, lake trout that feed extensively on rainbow smelt experience slower growth rates relative to lake trout that consume other species (Hassinger and Close 1984, Eby et al. 1995).

Despite lake trout predation on rainbow smelt, the introduction of rainbow smelt has caused lake trout population declines in a few systems. Specifically, lake trout recruitment declines after the establishment of rainbow smelt. Recruitment declines caused by rainbow smelt have been observed in lakes in Maine, Ontario, Vermont, Minnesota and even South Bay, Lake Huron (Hassinger and Close 1984, Evans and Loftus 1987, LaBar 1993). In Lake Champlain, rainbow smelt predation on lake trout larvae was thought to have been a factor in the extirpation of lake trout (Riley and Marsden 2009).Extensive rainbow smelt predation on lake trout larvae, however, has not been observed. In the two Minnesota lakes mentioned above, rainbow smelt diets were analyzed to determine to what extent they were preying on lake trout larvae. In total, of the 4,239 diets that were taken, only 2 lake trout larvae were discovered. This suggests the declines in lake trout were due to another mechanism such as a competitive interaction with rainbow smelt. It has long been believed that rainbow smelt compete with larval fish for plankton and other invertebrate resources critical to larval survival and development (Creaser 1929, Crowder 1980, Crowder et al. 1981). Given the lack of evidence of larval predation, a valid hypothesis is that rainbow smelt have a negative effect on lake trout through competition with adult rainbow smelt. However, no study to date has investigated this specific interaction between lake trout and rainbow smelt.

Unlike Atlantic salmon, larval lake trout are not spatially segregated from adult rainbow smelt. Lake trout move inshore or onto mid-lake reefs to spawn and do not require a stream (Ellrott and Marsden 2004). After overwintering, the eggs hatch early in spring. The fry quickly move into deeper water to begin feeding on crustaceans and insects (Deroche 1969, Hudson et al. 1995). The diets of juvenile (age-0 and age-1) lake trout are very similar to those of adult rainbow smelt and have the potential to exhibit substantial dietary overlap. Whitefish and cisco, both cold-water forage species, are thought to have similar competitive interactions with juvenile lake trout at high densities in Ontario lakes. These competitive interactions cause similar decreases in lake trout recruitment and growth rates that are seen when lake trout interact with rainbow smelt (Powell et al. 1986, Gunn et al. 1987, Evans and Olver 1995). Lake whitefish and cisco are both species that rainbow smelt are known to extirpate and functionally replace in systems. Therefore, observed declines in lake trout recruitment after rainbow smelt introductions are most likely the result of competitive interactions between lake trout larvae and rainbow smelt.

WALLEYE

Walleye is a popular sport species commonly found in lakes and rivers throughout the Midwestern United States and nearly all Canadian providences (Lee et al. 1980). Rainbow smelt and walleye are not known to occur natively together. Unlike Atlantic salmon or lake trout, walleye are a cool-water species, preferring a broad range of intermediate temperatures (Scott and Crossman 1973). If rainbow smelt are present, adult walleye will actively select rainbow smelt over other species for prey (Jones et al. 1994). Consuming large numbers of rainbow smelt also causes walleye body condition metrics to increase (Krueger and Hrabik 2005). Predation pressure on rainbow smelt by walleye is intense enough to even cause declines in rainbow smelt biomass (Johnson and Goettl Jr 1999, Krueger and Hrabik 2005). However, walleye populations rarely attain biomass levels necessary to completely eliminate smelt populations.

Walleye lakes that become invaded by rainbow smelt generally experience declines in walleye recruitment and ultimately population declines. For example, within 10 years of invasion by rainbow smelt, walleye recruitment was reduced to almost zero in 12 inland lakes in Wisconsin (Colby et al. 1987, Mercado-Silva et al. 2007). Similar declines in walleye YOY occurred in the Horsetooth Reservoir, Colorado after the introduction of rainbow smelt (Jones et al. 1994, Johnson and Goettl Jr 1999). There has also been evidence of rainbow smelt depressing walleye recruitment in the Great Lakes. In Lake Erie rainbow smelt are thought to have been a contributing factor to the collapse of the walleye stock there in the 1940s (Regier et al. 1969, Hartman 1973). In Green Bay, Lake Michigan there was a marked increase in walleye recruitment following a mass smelt mortality event during the winter of 1942-1943 (Van Oosten 1947).

The negative interaction between rainbow smelt and walleye likely occurs during the small window of the walleye's larval stage. When walleye are stocked as fry in lakes invaded by rainbow smelt, recruitment has been minimal, however when walleye fingerlings (approximately 40 mm) are stocked instead they are able to recruit in reasonable numbers (Colby et al. 1987). The lack of any negative effects on fingerling walleye indicates rainbow smelt are adversely affecting walleye during their larval stage. It's during this vulnerable time in a walleye's life that rainbow smelt are able to cause increases in walleye mortality and ultimately decreases in walleye recruitment.

The mechanism responsible for the declines of walleye remains unknown. Larval walleye spend 20-30 days consuming zooplankton in the pelagic zone after hatching early in the spring (Engel et al. 2002). During this time larval walleye habitat usage overlaps with post-spawn adult rainbow smelt. There are currently two competing hypotheses to explain the walleye recruitment declines. There may be a competitive interaction between larval walleye and adult rainbow smelt, similar to the interaction between YOY yellow perch (*Perca flavescens*) and rainbow smelt. Larval walleye consume cyclopoid copepods, calanoid copepods and large bodied cladocerans (*Daphnia*), all of which are consumed by rainbow smelt (Houde 1967, Graham and Sprules 1992, Gliwicz et al. 2004). Such dietary overlap makes a competitive interaction likely. The alternate hypothesis is that rainbow smelt may consume larval walleye, as they do with larval lake whitefish and cisco. However, to date, no studies have confirmed that walleye larvae are actually consumed by rainbow smelt. Either mechanism or even a combination of the two may lead to the documented declines in walleye recruitment.

DISCUSSION

The exact manner in which rainbow smelt interact with particular species is often dependent on the species in question, the specific system and the extent of habitat overlap. Differences in life history strategies are especially critical in determining how Atlantic salmon, lake trout and walleye interact with rainbow smelt. Of these three piscivores, only the juveniles of Atlantic salmon do not interact with rainbow smelt. Both Atlantic salmon and rainbow smelt are of the same marine origin and have had the opportunity to coevolve (Mandrak and Crossman 1992). Thus, it is not surprising that Atlantic salmon recruitment is not adversely affected by rainbow smelt in freshwater systems. Unlike Atlantic salmon, larval lake trout and walleye share the pelagic zone with the rainbow smelt. The specific life history strategy of both lake trout and walleye to rear larvae within the lake is vulnerable to the presence of a generalist pelagic competitor and/or predator such as rainbow smelt.

In larger systems it may be possible for these species to coexist without any detriment to the piscivores reviewed here. For instance, most the spawning activities of walleye and rainbow smelt in Lake Champlain occur in the southern basin, however after spawning the adults of both species return to the northern basin. The newly hatched YOY walleye occupy the southern basin where they grow and develop before entering the northern basin (Colby et al. 1987). The spatial segregation of the adult habitat and spawning habitat serves to limit larval walleye-adult rainbow smelt interactions, allowing the two species to coexist in Lake Champlain. Similar dynamics could occur in reservoirs with warm-water inputs. On the other hand, smaller systems create circumstances where interactions between rainbow smelt and walleye or lake trout larvae are likely to be more intense. The extent lake size and spatial configuration of spawning habitats plays in determining rainbow smelt-native fish interactions has not been formally evaluated. Future study should focus on how habitat size and configuration can influence rainbow smelt-piscivore interactions, which may explain some of the variation in piscivore response to rainbow smelt invasions.

The declines of walleye and lake trout presented here may be the result of a competitive or a predatory interaction. Although rainbow smelt are known to consume the larvae of lake whitefish and cisco, the lack of evidence of significant rainbow smelt predation on lake trout and walleye larvae suggests that a competitive interaction is more likely. The preference of rainbow smelt for large-bodied crustaceans can cause the zooplankton community to shift towards one dominated by smaller copepod zooplankton (Reif and Tappa 1966, Galbraith 1967, Beisner et al. 2003). The altered zooplankton community may create an "energetic bottleneck" for larval walleye and lake trout whose dietary ontogeny depend on specific zooplankton prey being available (Werner 1979).Similarly, in a whole lake manipulation Byström *et al.*(1998) discovered that introduced roach (*Rutilus rutilus*) were able to outcompete European perch (*Perca fluviatilis*) for key zooplankton resources, which resulted in slowed growth rates, increased mortality, and ultimately poor recruitment of YOY European perch. I believe similar "bottleneck" conditions exist for lake trout and walleye in some lakes that rainbow smelt have invaded.

One factor not examined in this study is the impact of thiamine deficiencies on lake trout and walleye egg success and larval survival. Rainbow smelt are known to carry high levels of thiaminase, an enzyme that metabolizes thiamine (Fitzsimons et al. 1999).

Predators that consume rainbow smelt and other forage fish high in thiaminase produce thiamine deficient eggs and larvae that experience early mortality syndrome (EMS). Salmonid recruitment success is known to be influenced by thiamine levels (Fisher et al. 1996, Honeyfield et al. 2005). Walleye embryo mortality has also been linked to thiamine levels (Barnes et al. 2005, Rinchard et al. 2011), suggesting that the consumption of rainbow smelt has caused declines in thiamine levels in spawning walleye, negatively affecting recruitment. The full extent to which rainbow smelt consumption affects walleye thiamine levels and recruitment success remains to be explored. However, it's expected that populations where rainbow smelt make up the primary diet item of adult walleye are at the highest risk to experience thiamine induced recruitment declines.

The European smelt (*Osmerus eperlanus*) and its interactions with pikeperch (*Sander lucioperca*), a close relative of walleye provide an interesting contrast to the examples presented here. The European smelt and pikeperch are similar in trophic ecology to rainbow smelt and walleye, respectively, in lakes throughout Northern Europe (Korlyakov and Mukhachev 2009). Unlike their North American counterparts, European smelt and pikeperch are both native to the same lakes. European smelt often make up a large proportion of pikeperch diets when the two species co-occur (Willemsen 1977, Keskinen and Marjomäki 2004). In these systems European smelt do not have a negative effect on pikeperch. One hypothesis that could explain this observation is that freshwater European smelt have relatively a short lifespan (max age = 3+) (Muus and Dahlstrröm 1967, Nellbring 1989) and small maximum size compared to freshwater rainbow smelt. In European freshwater systems smelt mature after their first year of life at only 90mm and rarely reach sizes over 120mm (Ivanova and Volodin 1981, Ivanova 1982, Nellbring 1989).

In North American lakes rainbow smelt readily attain this size, and begin to consume fish at 130 mm(Evans and Loftus 1987). In addition, after their spawning runs European smelt experience high levels of mortality (Muus and Dahlstrröm 1967, Korlyakov and Mukhachev 2009). The small size, earlier maturation and higher mortality likely limits interactions between the pikeperch and the European smelt. These differences in life history help explain why negative interactions do not occur between pikeperch and European smelt.

Rainbow smelt will continue to invade new freshwater systems across North America and alter native fish communities (Hrabik and Magnuson 1999, Mercado-Silva et al. 2006). Many of these alterations will have large negative consequences for culturally and economically important fisheries, such as those presented in this study. This study expands our current knowledge of how rainbow smelt interact with native freshwater piscivores. Although this information may help inform management decisions regarding established populations of rainbow smelt, preventing the spread of invasive species is often the most efficient means of control. The removal of invasive fish species after their establishment is often not biologically or economically feasible(Vander Zanden and Olden 2008). Preventative measures, such as public education, remain the best tools for managers to slow the spread of aquatic invasive species (Finnoff et al. 2006, Vander Zanden et al. 2010).

Table 1- Summary of case studies that examine rainbow smelt (*Osmerus mordax*) interactions with Atlantic Salmon (*Salmo salar*), lake trout (*Salvelinus namaycush*) and/or walleye (*Sander vitreus*). Interaction Codes: G - Increased growth rates, P - Smelt are preyed on, R - Recruitment declines

Lake(s)	Location	Smelt Population Status	Atlantic Salmon	Lake Trout	Walleye	Reference(s)
Sparkling Lake	Wisconsin	Introduced			R	Mercado-Silva *et al*. 2007; Roth *et al*. 2010
Beaver Dam, Cisco Lake, Crystal Lake, Dead Pike, Diamond Lake, Keyes Lake, Long Lake, Whitefish Lake	Wisconsin	Introduced			R	Mercado-Silva et al. 2007
Beech Hill Lake, Eagle Lake, Green Lake, Long Lake, Lower Pattern,	Maine	Native	P			Fuller and Cooper 1946
Devilfish Lake	Minnesota	Introduced		G,R		Hassinger and Close 1984

Table 1 (cont'd)

Lake(s)	Location	Smelt Population Status	Atlantic Salmon	Lake Trout	Walleye	Reference(s)
Fence Lake	Wisconsin	Introduced			G,R	Colby *et al*. 1987; Krueger and Hrabik 2005; Mercado-Silva *et al*. 2007
Lake Michigan	Illinois, Indiana, Michigan, Wisconsin	Introduced		P	R	Eby *et al.* 1984; Van Oosten 1947
Lake Ontario	New York, Ontario	Introduced		P		Eby *et al*. 1984; Mills *et al*. 2003
Horsetooth Reservoir	Colorado	introduced			G,R	Jones *et al*. 1994; Johnson and Goettl Jr. 1999
Lake Champlain	New York, Vermont	Native	P	R	P	Ellrott and Marsden 2004; Kirn and LaBar1996; Riley and Marsden 2009
Lake Eire	Michigan, New York, Ohio, Ontario, Pennsylvania	Introduced			R	Regier *et al*. 1969; Hartman 2000

Table 1 (cont'd)

Lake(s)	**Location**	**Smelt Population Status**	**Atlantic Salmon**	**Lake Trout**	**Walleye**	**Reference(s)**
Lucerne Lake	Wisconsin	Introduced			R	Colby *et al*. 1987; Mercado-Silva *et al*. 2007
Moosehead Lake	Maine	Introduced	P			Cooper and Fuller 1945
Schoodic Lake	Maine	Introduced	G			Havey 1973
Sebago Lake	Maine	Native	P	P		Kendall 1935; Boucher and Warner 2006
Various Lakes (> 100 total)	Maine	Native / Introduced	P	G		Boucher and Warner 2006; Johnson 2001
West Bearskin Lake	Minnesota	Introduced		G,R		Hassinger and Close 1984

Table 1 (cont'd)

Lake(s)	**Location**	**Smelt Population Status**	**Atlantic Salmon**	**Lake Trout**	**Walleye**	**Reference(s)**
Lake Superior	Minnesota, Wisconsin, Michigan, Ontario	Introduced		P		Eby *et al.* 1984; Ray *et al.* 2007
Lake Erie	Ohio, Michigan, Ontario, Pennsylvania, New York	Introduced			P,R	Hartman and Mangraf 1992; Hartman 1973; Regier *et al.* 1969
Lake Huron	Michigan, Ontario	Introduced		P		Bronte *et al.* 2003; Dobiesz *et al*. 2005

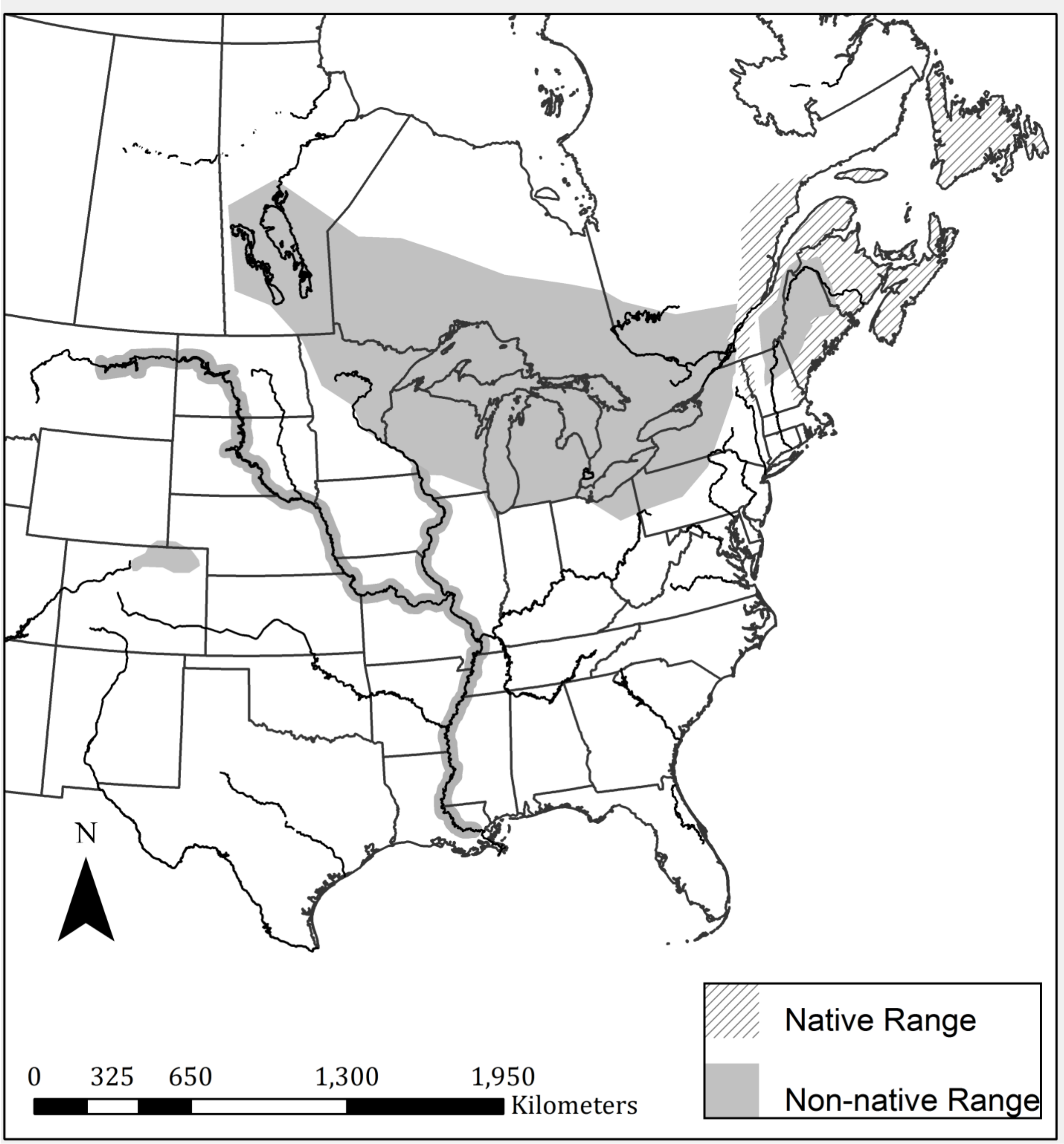

Figure 1 – The current North American distribution of rainbow smelt (*Osmeus mordax*) in both its native range extent (hashed boundaries) and non-native range extent (solid boundaries).

CHAPTER II

INTRODUCTION

The majority of sustainable fisheries are dependent on naturally reproducing fish. When natural reproduction alone cannot support a population, stocks are often enhanced through the stocking (Cowx 1998). However, Naturally reproducing stocks are more ecologically resilient and stable compared to populations that are supported by stocking (Holmlund and Hammer 1999).Additionally, stocking efforts are expensive to undertake and often consume substantial resources for natural resource management agencies. For those reasons, natural reproduction is often a desired trait of native, wild fish stocks. However, the processes that regulate natural reproduction are complex and not fully understood, which is evidenced by the natural variation we observe in recruitment over time (Houde 1987). Identifying these processes aids our ability to understand and predict natural reproduction, which provides valuable insights for the management of fish stocks. Reproductive success is often measured by year-class strength, which is typically regulated by high mortality rates fish experience during earliest part of their lives. Typical cumulative larval mortality rates regularly exceed 99%, but even small variations in this rate can have large impacts on recruitment (Houde 1987, Houde 1989). Known abiotic factors that contribute to these high mortality rates include temperature, wind, water level or flow rate, and habitat availability (Koonce et al. 1977). Biotic factors such as predation, competition, and cannibalism also contribute to high larval mortality rates (Weber et al. 2011). One of the most important biotic factors that contribute to larval mortality is prey abundance and composition. If prey required to advance ontogeny are rare or unavailable, larval mortality rates can increase and ultimately lead to weak year-class strength.

Walleye (*Sander vitreus*) are a species where prey abundance and composition have a large influence on larval growth and survival (Hoxmeier et al. 2004, Hoxmeier et al. 2006). Larval walleye follow a very specific zooplanktivorous dietary ontogeny for the first three to four weeks of their lives. After hatching and yolk absorption walleye begin feeding on cyclopoid copepods until they reach a size of approximately 13 mm. Within the size range of 13mm to 19mm larval walleye feed on larger calanoid copepods. At sizes larger than 19mm larval walleye feed primarily on large-bodied *Daphnia* species until they reach 35-40 mm, after which they begin feeding on benthic invertebrates (Houde 1967, Graham and Sprules 1992). Mayer and Wahl (1997) found that larval walleye fed a diet of copepods experienced significantly higher mortality rates than those fed *Daphnia* species. This indicates the significance *Daphnia* have on the successful completion of walleye dietary ontogeny and how a disruption in the progression of the zooplanktivorous ontogeny would lead to increased mortality rates.

There are several factors that may complicate and effective evaluation of larval walleye foraging and survival. If critical zooplankton resources are missing, large-scale mortality (> 60%) from starvation occurs in as little as five days (Jonas and Wahl 1997). Given such a short time period, sampling enough larval walleye to ascertain that zooplankton abundance or composition is limiting survival is unlikely. Sampling efforts can be further complicated by natural variation of the zooplankton community and walleye densities. Combined, these factors limit the effectiveness of empirical studies to test whether larval walleye growth and survival is limited by prey abundance and community composition. These limitations thus support to modeling approach that can limit the influence of exogenous factors on walleye recruitment.

Previous attempts to model larval walleye foraging and growth have not been flexible enough to adequately evaluate how prey zooplankton composition and density effect larval walleye survival. General bioenergetic models require diets to be known beforehand (Hanson et al. 1997) which, for the reasons above, is not a possibility in systems where zooplankton availability limits larval walleye survival. Although several studies have evaluated larval walleye foraging and diets (Houde 1967, Fox and Flowers 1989, Graham and Sprules 1991, Johnston and Mathias 1994b), it has not been fully incorporated into a bioenergetic model that could adequately evaluate growth and survival. Rose (1999) incorporated a foraging model into an individual based bioenergetic model for larval walleye in Lake Oneida, New York. However, the parameters for this foraging model were not derived from actual field observations.

I developed a linked foraging/bioenergetics model that evaluates how prey abundance and composition effects larval walleye growth and survival. The foraging model allows prey selectivity to vary according to the size of the larval walleye. Varying selectivities create the dietary ontogeny that has been described for larval walleye. Prey selectivities are found readily from field and laboratory studies in the literature. The foraging model also incorporates field-derived prey data in order to determine how abundance and composition affect larval foraging. Finally, the foraging model was integrated into a bioenergetics model to simulate growth of the larval walleye.

Lakes that are invaded with rainbow smelt (*Osmerus mordax*) provide an ideal opportunity to test the efficacy of such a model. Rainbow smelt are an invasive species to the Laurentian Great Lakes region. Since their establishment, rainbow smelt have negatively affected several native species, including walleye. Rainbow smelt are linked to declines of native pelagic fish such including lake herring (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*) in the Great Lakes as well as smaller inland lakes (Evans and Loftus 1987). The declines of these two species are likely caused by predation of their young-of-year (Loftus and Hulsman 1986) by rainbow smelt.

Competition for zooplankton resources may also affect some species. In Crystal Lake, Wisconsin, rainbow smelt caused a similar decline of yellow perch through competitive interaction with yellow perch (*Perca flavescens*) YOY (Hrabik et al. 2001). Similarly, walleye are known to experience recruitment declines after rainbow smelt invasions. In some systems, walleye recruitment fails entirely less than ten years following rainbow smelt establishment (Johnson and Goettl Jr 1999, Mercado-Silva et al. 2007). Currently, these declines in walleye recruitment are thought to be the consequence of rainbow smelt consuming larval walleye or due to a competitive interaction between larval walleye and rainbow smelt for zooplankton resources.

Rainbow smelt are visual feeders, actively selecting large-bodied zooplankton, which can cause dramatic shifts in the pelagic zooplankton community composition after an invasion (Reif and Tappa 1966). In Crystal Lake and Sparkling Lake, Wisconsin, rainbow smelt were able to drive *Daphnia* abundances to levels less than 50% of their pre-invasion densities. As a consequence, these lakes became almost completely dominated by copepods (Beisner et al. 2003). In Sporley Lake, Michigan, large-bodied *Daphnia* were replaced by smaller cladocerans and calanoids after the introduction of rainbow smelt (Galbraith 1967). The reduction in large-bodied *Daphnia* species creates a competitive release for small-bodied zooplankton, which leads to pelagic zooplankton community dominated by copepods and small cladocerans(Brooks and Dodson 1965). A zooplankton community lacking *Daphnia* would disrupt the dietary ontogeny of larval walleye that may lead to increased levels of larval mortality and ultimately to the observed recruitment failures.

In this study I evaluated how the composition of the pelagic zooplankton community can limit larval walleye growth and survival. I implemented a bioenergetic model that accounted for the ontogenetic shifts in prey preferences of larval walleye to evaluate how the conditions created by invasive rainbow smelt can limit walleye recruitment. I gathered zooplankton and larval walleye densities from lakes contrasting rainbow smelt populations in northern Wisconsin as a test of model performance. As a precaution, I also sampled rainbow smelt diets for any evidence of predation on larval walleye to evaluate whether predation could explain the lack of walleye YOY in smelt-invaded lakes. The results from this study provide useful insight on modeling larval walleye bioenergetics and foraging, as well as on the mechanism responsible for declines of walleye populations after rainbow smelt introductions.

METHODS

SITE SELECTION

This study was conducted in four lakes located in Vilas County, Wisconsin during the spring and summer of 2010 (Figure 2). Long Lake and Sparkling Lake both contain established populations of rainbow smelt while the other two, Plum Lake and Escanaba Lake, lack rainbow smelt. These lakes were selected due to their similarities in adult walleye densities and fish communities, as well as their relative proximity to one another (Table 2). All four lakes have similar densities of adult walleye, ranging from 4-6 individuals·acre^{-1}. These densities were maintained through a combination of natural reproduction and stocking efforts (Gilbert, WDNR, Vilas County, pers. comm.). Prior to rainbow smelt invasion, both Sparkling Lake and Long Lake supported fall YOY walleye densities similar to those found in Escanaba Lake and Plum Lake (Mercado-Silva et al. 2007, Cichosz 2009, 2010a, b). Given the similar densities of spawning adults and past recruitment patterns, I assumed that the reproductive potential of walleye was relatively equal across all four lakes.

ZOOPLANKTON COLLECTION AND PROCESSING

I sampled the pelagic zooplankton community once a week in each lake from May 1st 2010 to July 1st 2010 in order to monitor the zooplankton community that would be pertinent to zooplanktivorous larval walleye. All collections were done at the deepest point of each lake and conducted just before sundown. Zooplankton were collected using a 35 μm mesh Wisconsin-style net that was towed vertically through the entire water column at approximately 1 m·s^{-1}(Downing and Rigler 1984). All samples were immediately preserved in 95 percent ethanol after filtration.

In the laboratory the contents of all zooplankton samples were identified and enumerated. Samples were diluted to a known volume, approximately 100 ml – 150 ml depending on total numbers of zooplankton. Three 1 ml sub-samples were taken from each diluted sample using a Hensen-Stempel pipette. Within each sub-sample all zooplankton were identified to the family level and counted (Balcer et al. 1984). All zooplankton were identified using a binocular dissecting microscope and measured with the aid of *Z3*, a measuring program for use with microscope-mounted cameras (NTL-LTER 2009). A total of 15 individuals from each family were measured to obtain a mean length within each family for each sub-sample. Total body length was measured according to Culver et al. (1985) and Downing and Rigler (1984). The total number of individuals in each sample was estimated by averaging counts from sub-samples and extrapolating those numbers to the known volume of the whole sample. The mean length for each family was calculated from each sample and was used as input in length-weight regressions (Table 3) to determine the average dry weight (μg) of an individual from each family (Bottrell et al. 1976). The estimates of mean individual weight for each family were multiplied by the corresponding count data to assess the standing biomass of each family. Differences between lakes in mean length of calanoid copepods, cyclopoid copepods, and *Daphnia* were tested using ANOVA (α=0.05). The length data from each prey group was pooled across sampling dates to test for differences in mean length. Specific differences among lakes were examined further using Fischer's Least Significant Difference (α=0.05).

LARVAL WALLEYE SAMPLING

I assessed larval walleye abundances among lakes using standardized ichthyoplankton tows. Ichthyoplankton sampling was performed once a week after sundown from May 1st, 2010 to July 1st, 2010. The larval fish community was sampled using a side mounted ichthyoplankton net (550 μm mesh). Larvae were sampled at two transects in each lake. Transects were selected to incorporate known walleye spawning sites in each lake (Gilbert WIDNR pers. comm.). Tows were conducted parallel to the shore at both a 1m depth and at the surface (Engel et al. 2002). Counts of larval walleye were pooled by date and transect in each lake. Tows occurred at 1.5-2.0 $m \cdot s^{-1}$ for three minutes. The total amount of water filtered was determined using a mechanical rotary flowmeter mounted in the center of the net opening. All captured larvae were preserved in 95 percent ethanol for analysis in the laboratory. Collected larvae were identified to species enumerated. Up to 50 individuals from each species were measured for total length under a binocular dissecting microscope using either *Z3* (NTL-LTER 2009) for larvae < 20 mm, or a microscope-mounted micrometer for larvae > 20 mm.

RAINBOW SMELT DIETS

Rainbow smelt diets were collected once a week from May 1st, 2010 to July 1st, 2010 in Sparkling Lake and Long Lake. Rainbow smelt were sampled using 30m experimental mesh horizontal gill nets. Mesh sizes in each net ranged from 13 mm to 25mm (bar). Each net was set perpendicular to the shoreline and covered depths of 9m to 18m (Emery 1973, Nellbring 1989). Each net was allowed to soak for no longer than three hours starting at dusk. Gillnets were soaked after dark to coincide with the nightly diel vertical migration of rainbow smelt, during which they feed heavily (Burczynski et al. 1987). The short set time was necessary to preserve the diet contents, specifically to prevent digestion of walleye larvae. After the smelt were removed from the net, any surviving fish were euthanized with an overdose of MS-222. Immediately following euthanization, smelt body cavities were injected with 95% ethanol and the fish were placed on ice to further slow digestion. After return to the laboratory, the entire digestive tract was removed and preserved in 95% ethanol.

Rainbow smelt diets were analyzed to determine if larval walleye were consumed. Vertebrate and insect diet items were identified to species whenever possible and enumerated. All zooplankton diet items were identified to family, and ten individuals from each family were measured. The average individual zooplankton length from each family was used to determine the average individual dry weight (μg) using the same regression equations above (Table 3). The average individual dry weight was multiplied by the total number of individuals to estimate the total dry weight of zooplankton prey. All other non-planktonic prey items were placed in a drying oven for at least 24 hours to determine their dry weights.

MODEL DESCRIPTION

I used a bioenergetics-based foraging model to evaluate larval walleye growth and survival in all four study lakes. The goal of the model was to test whether the zooplankton community composition has an effect on larval walleye survival and growth. Specifically, the model simulates an individual larval walleye for 30 days after first feeding. Inputs to the model include field-derived larval walleye foraging and zooplankton community data. All simulations were run for 30 days starting on 5/15/10 (DOY=135), with daily time steps. The start date represents the approximate date just before larval walleye densities peaked in all four lakes (see results section below). The length of the simulation also reflects the first month of larval walleye life when their diet is almost exclusively comprised of zooplankton and thus most likely to overlap with the diet of rainbow smelt (Graham and Sprules 1992, Engel et al. 2002).

An energetic bottleneck occurs when larval walleye growth is considerably slower or stops due to a lack of suitable prey items. Several outputs of the model will help determine if a bottleneck for larval walleye is possible in the smelt invaded lakes. At the end of each time step the model reports the simulated larval walleye's weight (g), proportion of maximum consumption achieved (p-value), and relative diet proportions. This model is designed that if a simulated larval walleye's weight is less than 0.2054 g (~30 mm) I assume an energetic bottleneck exists. The p-value and relative diet proportions allow me to assess how much the simulated larval walleye consumed and to determine which prey item is limiting to the growth and development of the larval walleye. I expect a bottleneck to exist in the rainbow smelt invaded lakes, Sparkling Lake and Long Lake due to the presence of rainbow smelt in those systems.

The bioenergetic portion of the model was based on the Hanson et al. (1997)Wisconsin model. The bioenergetic parameters used were taken from Madon and Culver (1993). Temperature data were gathered from an instrumented buoy in Sparkling Lake for all dates considered. Surface water temperature was collected at the deepest part of the lake once an hour as part of the LTER-North Temperate Lakes (http://lter.limnology.wisc.edu/) protocol (Figure 3). I used the average daily value in each step in the simulation. Because I am only interested in determining how zooplankton community composition affects larval walleye growth, temperature data were held constant for each simulation to eliminate temperature as a possible confounding variable. Growth (G) was determined at each time step (t) using the discrete form of the bioenergetics equation:

$$G_t = C_{r,t} - R_t - F_t - U_t - S_t \tag{1}$$

where C is consumption, r modifies C to be realized consumption, R_t is the predicted respiration rate, F_t is the predicted excretion rate, U_{te} is the predicted egestion rate, and S_t is the predicted standard dynamic action rate. All rates above were calculated in J·g^{-1}·d^{-1} in wet mass. Total weight changes are given by:

$$W_{t+1} = W_t + \left(\frac{G_t \cdot W_t}{E_{pred}} \right) \tag{2}$$

where W represents the weight at time step t and E_{pred} is the energy density of larval walleye (3349 J·g^{-1}; (Madon and Culver 1993). It should also be noted that all length-weight conversions followed the relationship:

$$L = a \cdot W^{b} \tag{3}$$

with a = 49 and b = 0.31 (Rose et al. 1999).

REALIZED CONSUMPTION, C_r

Consumption rates for each prey item j were based on a variant of Holling's (1965) multispecies Type II functional response, following (Johnston and Mathias 1994b):

$$C_{j,t} = \frac{C_{\max,t} \cdot \left(9 \cdot P_{j,t} \middle/ D90_{j,L} \right)}{1 + \sum_{j=1}^{n} \left(9 \cdot P_{j,t} \middle/ D90_{j,L} \right)} \qquad (4)$$

where *Cj,t* is the potential consumption rate (g·g^{-1}·d^{-1}) of prey type *j*. *Pj,t* is the environmental prey density (µg·l^{-1} dry weight) of prey *j* at time *t*. *Cmax,t* is the maximum consumption rate which is a temperature dependent function of body size. *D90j,L* is the density of prey at which a larval walleye of length *L* is 90% of *Cmax*. The *D90j,L* is a saturation parameter that changes with length to allow larval walleye diet preferences to change as they grow. Prey for these simulations included the primary diet items for larval walleye: calanoid copepods, cyclopoid copepods and *Daphnia* (Houde 1967, Graham and Sprules 1992). The realized consumption rate (J·g^{-1}·d^{-1}) is given by the equations:

$$C_{r,t} = \sum_{j=1}^{n} \left(C_{j,t} \cdot V_t \cdot E_{prey,j} \right) C_{r,t} = \sum_{j=1}^{n} \left(C_{j,t} \cdot V_t \cdot E_{prey,j} \right) \qquad (5)$$

$$V_t = \frac{100 - \left(a_V \cdot e^{\left(b_V \cdot L_t \right)} \right)}{100} \qquad (6)$$

where $E_{prey,j}$ represents the energy density (j·g^{-1} dry mass) for each prey type *j*. For these simulations D_{prey} values were 2100 J·g^{-1} for both copepod groups and 2600 J·g^{-1} for *Daphnia*(Hanson et al. 1997). Capture success, *V*, is an allometric function that varies between 0 and 1 with the constants a_V and b_V. Both a_V (338.45) and b_V (-0.16) were derived from laboratory experiments by Johnston and Mathias (1994a). They were able to demonstrate that capture success of zooplankton increases logarithmically with size for larval walleye, independent of temperature. The capture efficiency approaches 1 at sizes slightly larger than 20 mm. V_t allows the foraging model to account for the observed poor capture success of larval walleye at smaller sizes and to make the realized consumption rate more accurate for larval walleye.

D90 PARAMETER ESTIMATION

$D90_{j,L}$ values for each prey type *j* were determined by length-dependent functions. All the zooplankton densities, $P_{j,t}$, from each lake were pooled and used to determine $D90_{j,L}$ values for each of the three of the larval walleye size classes for each prey type *j* (Table 4). These functions were necessary to allow the diet composition and prey preferences to change with larval walleye size. Length-dependent functions of $D90_{j,L}$ are not available in the literature, so they were derived from field observations. Deriving functions to describe how $D90_{j,L}$ values change with size requires an estimate of prey selectivity, relating environmental prey biomass to diet proportions and deriving D90 values for each prey *j* at each size interval (table 4).

The single species type II functional response equation that is the underlying basis for eq. 4 is:

$$C_{j,t} = \frac{C_{r,t} \cdot 9 \cdot P_{j,t}}{D90_{j,L} + 9 \cdot P_{j,t}} \tag{7}$$

When each side of the eq. 7 is divided by $C_{r,t}$ the equation becomes:

$$e_{j,t} = \frac{C_{j,t}}{C_{r,t}} \tag{8}$$

$$e_{j,t} = \frac{9 \cdot P_{j,t}}{D90_{j,L} + 9 \cdot P_{j,t}} \tag{9}$$

where $e_{j,t}$ is the proportion of the larval walleye diet comprised of prey j at time step t. This arrangement allows me to relate zooplankton prey densities, $P_{j,t}$, with the diet proportion, $e_{j,t}$, of prey j. Equation 9 also enables me to directly estimate D90 values given field-derived values of $P_{j,t}$ and estimates of $e_{j,t}$.

Values of $e_{j,t}$ were derived from empirical observations of selectivity found in the literature. Estimates of larval walleye selectivity at three different sizes were taken from

Graham and Sprules (1992) (Table 4). Selectivities are given for three size intervals of larval walleye: 9-13mm, 13-19mm, and 19-40mm. Each interval represents a different dietary ontogenetic step of larval walleye, which is reflected in the shifts in prey preference. The selectivity index used in both Graham and Sprules (1992) and this study was Manly's β (Manly 1973):

$$\beta_{j,t} = \frac{e_{j,t} / a_{j,t}}{\sum_{j=1}^{n} \left(e_{j,t} / a_{j,t} \right)} \tag{10}$$

$$a_{j,t} = \left(\frac{P_{j,t}}{\sum_{j=1}^{n} P_{j,t}} \right) \tag{11}$$

where $a_{i,t}$ is the proportion of prey type j in the environment. After inserting the $\beta_{j,t}$ from

In order to estimate $e_{j,t}$ eq. 10 was rearranged to:

$$\sum_{j=1}^{n} \left(e_{j,t} / a_{j,t} \right) = \frac{e_{j,t} / a_{j,t}}{\beta_{j,t}} \tag{12}$$

Under this arrangement the differences between the summation terms (left side eq. 12) for each prey item could be simultaneously minimized to estimate $e_{j,t}$ for the relative zooplankton prey densities, $a_{j,t}$ in each time step. The minimization process was conducted in MATLAB using the *fminsearch* function (Mathworks 2008). For each minimization routine every combination of e_j (values between 1 and 0, at 0.1 intervals) that summed to 1 were used as starting points. This was done to ensure that the global minimum was found while estimating all three e_j parameters simultaneously. This process was repeated using all the field zooplankton data from all four lakes for each of three larval walleye size intervals to estimate consumption given the known selectivities (Table 4). Ultimately, I estimated a value of $e_{j,t}$ for every value of $P_{j,t}$ that was collected in all four lakes during the spring of 2011.

Estimates of $e_{j,t}$ and their associated values of $P_{j,t}$ for all three length intervals enabled me to directly estimate $D90_{j,L}$using eq. 9. Values of $D90_{j,L}$ were estimated using non-linear least squares regression. This process was conducted for each prey type *j*, in each length interval considered (Figure 4). The result was three D90 values (one for each size interval) for each taxa of zooplankton prey *j*. All the values of $D90_{j,L}$ (three for each prey item *j*) were fit with curves to relate how the D90 values change with walleye length.

$$D90_{calanoid,L} = \left\lfloor ca_1 + \left[ca_2 \cdot \left(\frac{L_t - 16}{\left| L_t - 16 \right|} \right) \right] \right\rfloor \cdot \left(L_t - 16 \right)^2 + 6.757 \qquad (13)$$

$$D90_{calanoid,L} = \frac{cy_1 \cdot e^{\left(cy_2 \cdot L_t\right)}}{1 - \left(cy_1 / 1.367 \cdot 10^5 \right) + \left(cy_1 / 1.367 \cdot 10^5 \right) \cdot e^{\left(cy_2 \cdot L_t\right)}} \qquad (14)$$

$$D90_{daphnia,L} = da_1 \cdot e^{\left(-\left(L_t - 16\right)^2 / da_2 \right)} + 2.788 \qquad (15)$$

The parameters of each of these curves were derived and fit using a non-linear least squares procedure (Table 5). An effort was made to select curves that would fit the data and were biologically relevant to larval walleye growth and development (Figure 5). The shapes of these curves ultimately make ontogenetic diet shifts of larval walleye possible in the simulation.

This approach requires several assumptions regarding selectivity. First, I assume that the selectivity $\beta_{j,t}$ is constant for each prey type *j* in each of the three larval walleye size classes. I also assume that the selectivities I used are transferrable across systems. The selectivities found in table four were measured in Lake Oneida, which has very similar zooplankton community as each of the lakes in this study. It's reasonable to assume larval walleye would forage in a similar manner, given the similarity of the species present, between the lakes in this study and Lake Oneida. Lastly, I assume the relationships between $D90_j$values and length *L* are continuous rather than discrete. Continuous functions allow D90 values, and thus diet proportions, to change smoothly as the larval walleye grows. It's reasonable to expect that diet proportions don't change sharply, rather they transition smoothly.

SENSITIVITY ANALYSIS

I conducted a sensitivity analysis to evaluate how sensitive the model was to each of the derived D90 curve parameters. The model was run while each parameter (Table 5) was individually adjusted by both +10% and -10% while the other parameters and variables were kept static. The zooplankton densities from Escanaba Lake were used for each sensitivity analysis. The final length of a modeled larval walleye from Escanaba Lake (with no parameter adjustments) was used as the comparative baseline. The model was considered sensitive to a parameter if the baseline final larval walleye length varied disproportionately (> ±10%) to the parameter adjustment.

RESULTS

LARVAL WALLEYE DENSITIES

During the entire sampling period larval densities were lower in lakes containing rainbow smelt. Larval walleye catches (individuals·m^{-3}) peaked in each lake in late May (DOY = 140) (Figure 6). The declines in catch rates after the peaks was the result of the larval walleye beginning to feed on benthic invertebrates and after which they become less vulnerable to pelagic ichthyoplankton sampling (Galarowicz et al. 2005).Overall, the peak larval walleye densities were much lower in Sparkling Lake and Long Lake, the lakes with established populations of rainbow smelt. In Plum Lake, larval walleye densities peaked on

May 26th (DOY= 146) at 2.8 individuals·m^{-3}. Similarly, larval walleye densities reached 0.81 individuals·m^{-3} on May 31st (DOY=151) in Escanaba Lake. Peak larval walleye densities were much lower in Sparkling Lake and Long Lake at 0.18 and 0.12 individuals·m^{-3}respectively. All larval walleye caught in the ichthyoplankton tows were between 8 mm and 25 mm.

RAINBOW SMELT DIETS

Rainbow smelt diets were dominated by either crustaceans or insects in both Long Lake and Sparkling Lake. In Long Lake the rainbow smelt caught ranged in size between 110 and 150 mm (Table 6). I found no fish or fish larvae remains in any of the 86 diets that were analyzed from Long Lake. The primary diet items, by dry weight, for rainbow smelt in Long Lake were *Daphnia*, *Chaborus* and other dipterans. The rainbow smelt sampled in Sparkling Lake were smaller, ranging in size from 70 to 100 mm, with most falling between 80-90 mm. Similarly to Long Lake, there was no fish or fish larvae found in any of the 72 diets that were analyzed. By dry weight, *Daphnia* were a relatively small component of the diets of the rainbow smelt from Sparkling Lake. These smelt relied more on cyclopoid copepods and *Chaborus*.

ZOOPLANKTON COMMUNITIES

Trends in the total zooplankton biomass varied between each lake (Figure 7). In rainbow smelt invaded Long Lake and Sparkling Lake total zooplankton biomass (µg/l) respectively decreased and increased during the sampling period. Lakes without rainbow smelt saw a decline in total zooplankton biomass in Escanaba Lake and an incline in Plum Lake. With the exception of the last ten days (DOY = 160-170), zooplankton biomass in Sparkling Lake less than half of the zooplankton biomass found in the other three lakes. There was a clear distinction in composition of the zooplankton community between the lakes with rainbow smelt and those without rainbow smelt. In Long Lake, the zooplankton community was dominated by calanoid and cyclopoid copepods (Figure 8). Together, copepods composed of over 60 percent of the total pelagic zooplankton biomass on every sample date in Long Lake with cyclopoid copepods making up the majority of the biomass in every sample date. Copepods were also dominant in Sparkling Lake. Calanoid copepods were the most abundant zooplankton during the entire season, often comprising > 75% of the total biomass in Sparkling Lake. Conversely, in Escanaba and Plum Lakes, *Daphnia* biomass was a much larger component of pelagic zooplankton biomass. Over half the biomass in Plum Lake was made up of *Daphnia*. In Escanaba there was an increase of the proportion *Daphnia* that peaked at almost 80 percent, which abruptly decreased after May 31st (DOY=151).

Results from the ANOVA tests indicated that significant differences of mean lengths of calanoid copepods, cyclopoid copepods and *Daphnia* exist between lakes. There were significant differences in the average length of *Daphnia* between the lakes ($F_{3,632}= 65.395$, $p=< 0.001$). Fisher's LSD indicated that the *Daphnia* in Long Lake and Sparkling Lake were significantly smaller than those found in Escanaba Lake or Plum Lake (Figure 9).Although there were significant differences of mean length for the calanoid copepods ($F_{3,814}$ =

20.588, $p = < 0.001$) and cyclopoid copepods ($F_{3,858}$= 15.336, $p = < 0.001$) between lakes, I did not observe a pattern similar to *Daphnia* across lakes(Figure 9).

MODEL RESULTS

Modeled larval walleye growth was similar in each lake except Sparkling Lake. The model indicates that after 30 days larval walleye grew to over 30 mm in all the lakes except Sparkling Lake. In Sparkling Lake, the predicted final length of the larval walleye was only 23 mm (Figure 10). The p-values (the proportion of C_{max}) for the larval walleye in Sparkling Lake were among the lowest from all the lakes, and were especially low in the first 15 days of the simulation (Figure 11). Such low p-values demonstrate that the larval walleye in Sparkling Lake were not consuming enough to grow in the same manner as in the other lakes.

The inferred diets of the simulated larval walleye followed a similar progression as growth(Figure 12). At the beginning of the simulation larval walleye diets were dominated by cyclopoid copepods. At sizes around 11 mm, calanoid copepods began to replace cyclopoid copepods, such that by 16 mm, walleye diets were comprised almost exclusively of calanoid copepods. At sizes larger than 16 mm *Daphnia* began to be incorporated into diets, until they became the primary diet item. *Daphnia* never became a significant part of the diets of the modeled larval walleye in Sparkling Lake because these larvae never grew to a size large enough to consume them despite the smaller size of *Daphnia* in Sparkling Lake compared to Escanaba or Plum lakes.

MODEL SENSITIVITY ANALYSIS

The sensitivity analysis identified 3 parameters, one from each of the derived equations for the D90 curves, to which the model was sensitive (Figures 14 & 15). The sensitive parameters were the shape parameters (ca1, cy2 and da2) from each curve were. The shape of the D90 curves ultimately determines how quickly or slowly the larval walleye's prey preferences change with length. In each instance, when the shape parameter was lowered, it caused the final length of the larval walleye to increase. Lowering the value of the shape parameters causes the larval walleye to consume more of the prey across every length because saturation parameter, the *D90* value. In the case of cy2, raising the parameter value caused a disproportionate decrease in size because the D90 curve became steeper. This causes the larval walleye to consume less calanoid copepods across each size.

DISCUSSION

The spread of rainbow smelt in the Great Lakes region has, and will most likely continue to, put populations of walleye at risk of recruitment failure (Mercado-Silva et al. 2006). Invasive rainbow smelt affect native communities on multiple trophic levels (DeVries and Stein 2007), which can obscure the processes underlying their successful establishment. Not all walleye populations respond to rainbow smelt invasions identically (Regier et al. 1969, Kirn and LaBar 1996, Mercado-Silva et al. 2007). Thus, a comprehensive knowledge of important processes necessary for their establishment will help inform predictions of potential impacts in other systems. Identifying systems at higher risk of negative impacts of rainbow smelt is especially important considering the limited ability of scientists and managers to effectively monitor the large number of lakes in areas susceptible to smelt introductions.

The observed larval walleye densities in my study lakes provide further evidence that rainbow smelt populations can increase walleye mortality during their brief larval stage. The larval walleye densities in Long Lake and Sparkling Lake, both with rainbow smelt populations, were much lower compared to the lakes without rainbow smelt populations. This supports the observations that reductions in YOY walleye in rainbow smelt lakes occurs early in walleyes' life history (Colby et al. 1987, Nellbring 1989, Rooney and Paterson 2009). Recruitment success and larval dynamics of walleye can be highly variable (Madenjian et al. 1996, Hansen et al. 1998) and synchronous across regional spatial scales from 50 km to 1000 km (Colby et al. 1979, Myers et al. 1997). The similarity in spawning potential and historical fall YOY walleye also provides evidence that the low larval walleye densities seen in Long Lake and Sparkling Lake are not simply due to natural variation, and are likely a consequence of interactions with rainbow smelt in these lakes.

The composition of the pelagic zooplankton community likely contributed to the lower larval walleye densities found in Long Lake and Sparkling Lake. In both lakes copepods were the dominant zooplankton taxa. In laboratory studies, small larval walleye (< 8-10 mm) fed exclusively copepod prey experienced significantly higher mortality rates than those larvae fed exclusively on *Daphnia* species (Mayer and Wahl 1997). There is evidence that the growth of larval yellow perch is limited by the presence of cladoceran prey as well (Mills et al. 1989, Adeyemo et al. 1994, Fulford et al. 2006).

The total biomass of zooplankton may have limited the survival of larval walleye in Sparkling Lake. Depressed zooplankton biomass can lead to poor larval survival and year class development (Morsell and Kempinger 1971, Storck and Miller 1982), as was observed in Lake Oahe, South Dakota following smelt establishment (Fielder 1992). Although rainbow smelt are demonstrated to alter the composition of zooplankton communities, there is equivocal evidence to support the notion that they suppress the total biomass of the zooplankton community.

I found no evidence for the predation by rainbow smelt on larval walleye. There were no larval walleye in over 150rainbow smelt diets I collected from Sparkling Lake and Long Lake. The lack of walleye larvae in smelt diets is consistent with other studies, but it is unknown if detecting rainbow smelt predation on larval walleye is possible. For instance, walleye may be digested in rainbow smelt stomachs in under an hour, as other authors have indicated(Colby et al. 1987). During the larval stage, walleye contain few hardened structures or other distinguishing characteristics (such as pigmentation) (McElman and Balon 1979)that would clarify their presence in diets. Other species such as cisco and lake whitefish that are known to be consumed by adult rainbow smelt hatch at sizes almost twice the size of walleye (Auer 1982). Their increased size and faster larval development would likely make them more detectable in diet analyses. In the case that larval walleye are detectable in rainbow smelt diets, larger sample sizes would be recommended to detect rainbow smelt predation. Future studies should aim to increase diet sample sizes and take further actions to prevent digestion to definitively rule rainbow smelt predation on larval walleye out.

The results from the model suggest that an energetic bottleneck exists in Sparkling Lake but not Long Lake. Walleye typically grow to sizes greater than 30 mm during their first month of life (Houde 1967, Graham and Sprules 1992, Engel et al. 2002). Only the modeled larval walleye from Sparkling Lake did not reach this size at the end of the simulation. This is likely the result of the lower zooplankton biomass in combination with a calanoid copepod-dominated zooplankton community found in Sparkling Lake. An energetic bottleneck can prolong the larval stage due to slower growth, which can ultimately lead to higher mortality rates of YOY walleye (Werner 1979). My model predicted slower growth rates in Sparkling Lake as a result of the zooplankton community composition. This suggests that an energetic bottleneck existed that could prohibit adequate conditions for walleye survival. Further, predation was likely low in this lake. During field sampling for rainbow smelt diets, I only encountered individuals between 70 and 90 mm. Rainbow smelt are not known to consume fish until they reach at least 130mm (Maccrimmon and Pugsley 1979, Evans and Loftus 1987).

The modeled growth of larval walleye in Long Lake was similar to the growth seen in Escanaba Lake and Plum Lake. The zooplankton biomass was high enough to avoid an energetic bottleneck despite a zooplankton community skewed heavily towards calanoid copepods. However, larval walleye densities were still low in this lake. It appears some other unaccounted variable was responsible for the low larval walleye densities. One possibility not examined in this study is a predatory or competitive interaction between larval walleye and other species. For example, high densities of adult yellow perch are known to limit walleye recruitment in small lakes (<500 ha) in Northern Wisconsin(Hansen et al. 1998, Beard Jr et al. 2003). However, it remains unknown how the introduction of rainbow smelt affects larval walleye interactions with other native species.

Thiamine deficiency could also be responsible for the lowered larval densities. Thiaminase, an enzyme that breaks down thiamine, is found in the tissues of rainbow smelt

(Fitzsimons et al. 1999). The consumption of rainbow smelt by adult walleye may decrease thiamine levels in eggs and larvae, which can lead to early mortality syndrome (EMS) (Rinchard et al. 2011). Rainbow smelt are known to cause EMS in Salmonids (Fisher et al. 1996, Honeyfield et al. 2005), however it remains unknown to what extent the consumption of rainbow smelt effects thiamine levels in the eggs and larvae of walleye.

The model used in this study expands on previous larval walleye bioenergetic models to include ambient prey abundances as a factor in determining diets. Prior models had not considered zooplankton selectivity or the dietary ontogeny of larval walleye (Madon and Culver 1993, Johnston and Mathias 1994b, Rose et al. 1999, Post 2007). These considerations allow this model to evaluate how both prey density and composition impact larval walleye energetics and growth. This model could be improved by incorporating estimates of selectivity from more sizes into the derivation of the D90 curve. This would create more data points to fit the D90 curves to, which would in turn make the shapes of the D90 curves and their parameter estimates more accurate and perhaps less sensitive. This approach could easily be applied to other species such as lake trout that are also affected by rainbow smelt (Hassinger and Close 1984, Riley and Marsden 2009)

Rainbow smelt are able to impact multiple trophic levels, and thus could be considered keystone species (Paine 1980) in some lakes they invade. Rainbow smelt have the ability to limit the abundance their predators through mechanisms described in this paper. Simultaneously, rainbow smelt can alter the zooplankton community to one that is amenable to their own success. These types of effects are known as “middle-out” effects (Johnson and Goettl Jr 1999, DeVries and Stein 2007), can make deciphering food-web interactions particularly difficult.

The focus of this study has been on the effects of rainbow smelt on a single species, however rainbow smelt affect many species (Nellbring 1989, Rooney and Paterson 2009). Many of these impacts on native species, such as walleye, are not well understood or remain to be documented. Many lakes in the Great Lakes region are suitable for rainbow establishment (Mercado-Silva et al. 2006). Eradicating invasive species after their establishment is often not a realistic possibility for managers (Lodge et al. 2008). Thus, quantifying impediments to natural reproduction for top predator species can help define where restoration efforts, such as stocking, are likely to be most valuable.

Table 2 - Lake information from study lakes.

Lake	**Max. Depth (m)**	**Mean Depth (m)**	**Shoreline (km)**	**Area (km2)**	**Year Rainbow Smelt (*Osmerus mordax)* Introduced**	**Other Common Species ***
Escanaba Lake	7.92	4.27	8.40	1.23	Not present	BLG, PKS, MSK, NPK, LMB, WEE, YWP
Long Lake	28.96	9.14	13.20	3.59	1985	BLG,LMB, SMB, MSK, NPK, WEE, YWP
Plum Lake	17.37	6.04	23.30	4.28	Not present	BLG, PKS, MSK, NPK, LMB, SMB, WEE, YWP
Sparkling Lake	19.51	NA†	3.35	0.64	1981	BLG, PKS, MSK, SMB, WEE

* BLG = Bluegill (*Lepomis macrochirus*), PKS = Pumpkinseed (*Lepomis gibbosus*), MSK = Muskellunge (*Esox masquinongy*), NPK = Northern Pike (*Esox lucius*), LMB = Largemouth Bass (*Micropterus salmoides*), SMB = Smallmouth Bass (*Micropterus dolomieu*), WEE = Walleye (*Sander vitreus*), YWP = Yellow Perch (*Perca flavescens*)

† Data not available

Table 3 - Coefficients for length(mm)-dry weight(μg) regressions for the different taxa of zooplankton sampled. Regressions took the form: $W=aL^{b}$.

Taxa	**a**	**b**	**Source**
Bosmina	21.97	3.04	Bottrell et al. 1976
Calanoid	7.72	2.33	Dumont et al. 1975
Chydorid*	9.93	2.24	Malley et al. 1989
Cyclopoid	6.48	2.59	Dumont et al. 1975
Daphnia	4.95	2.84	Bottrell et al. 1976
Holopedium	6.13	2.74	Malley et al. 1989
Polyphemidae	6.93	2.15	Dumont et al. 1975
Sididae	3.58	3.24	Malley et al. 1989

* Coefficients derived from the data given. All other coeficients were taken directly from the literature.

Table 4 - Values of manly's β, taken from Graham and Sprules (1992), used in the estimation of consumption (e_j) values (eqs. 13 & 14) for laval walleye (*Sander vitreus*) feeding on the three taxa listed below.

	Walleye Length (mm)		
Taxa	**10 - 13**	**13 - 19**	**19 - 40**
Calanoid	0.150	0.920	0.049
Cyclopoid	0.800	0.070	0.001
Daphnia	0.050	0.010	0.950

Table 5 - Descriptions, symbols and values for parameters used in equations 11-13.

Parameter	Symbol	Value
Baseline calanoid shape parameter	ca_1	8.5503
Modifying calanoid shape parameter	ca_2	-6.226
Cyclopoid *D90* value at Length = 0	cy_1	1.11E-05
Cyclopoid shape parameter	cy_2	1.167
Peak value of *Daphnia* curve	da_1	4323.9
Daphnia shape parameter	da_2	38.033

Table 6 - Relative diet proportions (% dry weight) by length of all rainbow smelt (*Osmerus mordax*) caught in Long Lake and Sparkling Lake during the spring of 2010.

		Long Lake Rainbow Smelt length (mm)				**Sparkling Lake Rainbow Smelt length (mm)**		
		110 - 120 (n=4)	120 - 130 (n=29)	130 - 140 (n=39)	140 -150 (n=14)	70 - 80 (n=10)	80 - 90 (n=54)	90 - 100 (n=8)
	Taxa							
Cladocera								
	Bosmina	0.16	0.17	0.14	0.23	13.35	13.90	4.58
	Daphnia	23.80	90.00	33.14	38.11	-	0.07	0.15
	Polyphemus	19.00	1.49	11.14	9.76	3.65	9.59	0.19
	Other	0.08	0.01	0.04	0.00	0.01	0.26	0.52
Copepoda								
	Calanoid	-	0.04	0.05	0.04	2.79	19.85	0.65
	Cyclopoid	0.06	3.90	5.77	0.75	46.12	22.83	21.71
Diptera								
	Chaborus	-	3.63	36.99	51.10	28.80	33.49	72.20
	Other Dipteran	56.90	0.76	12.74	-	5.28	-	-

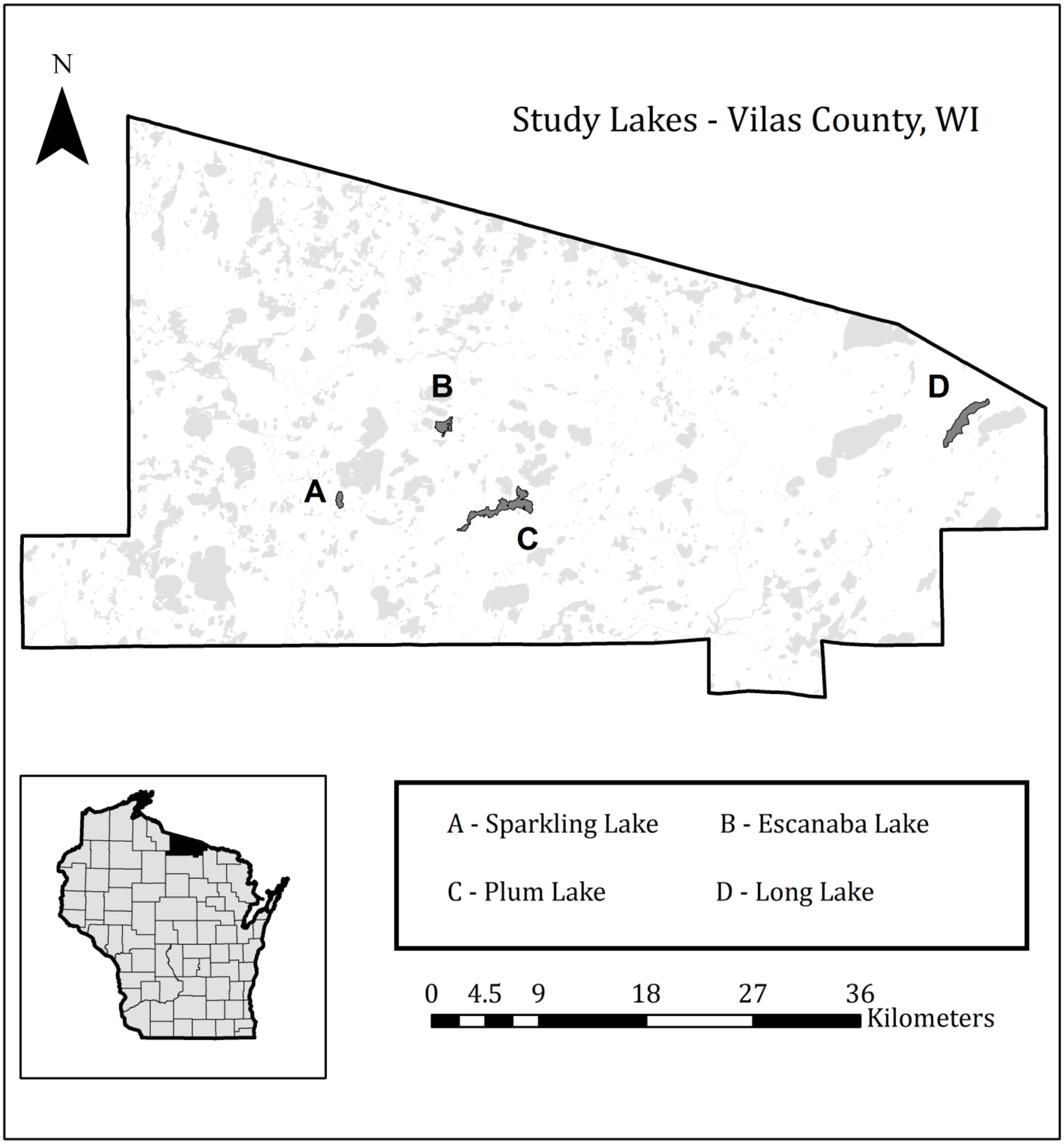

Figure 2 – A map of Vilas County, Wisconsin that displays the locations of all four study lakes. Sparkling Lake (A) and Long Lake (D) both have smelt populations, while Escanaba Lake (B) and Plum Lake (C) lack smelt populations. Refer to table 1 for lake specific information.

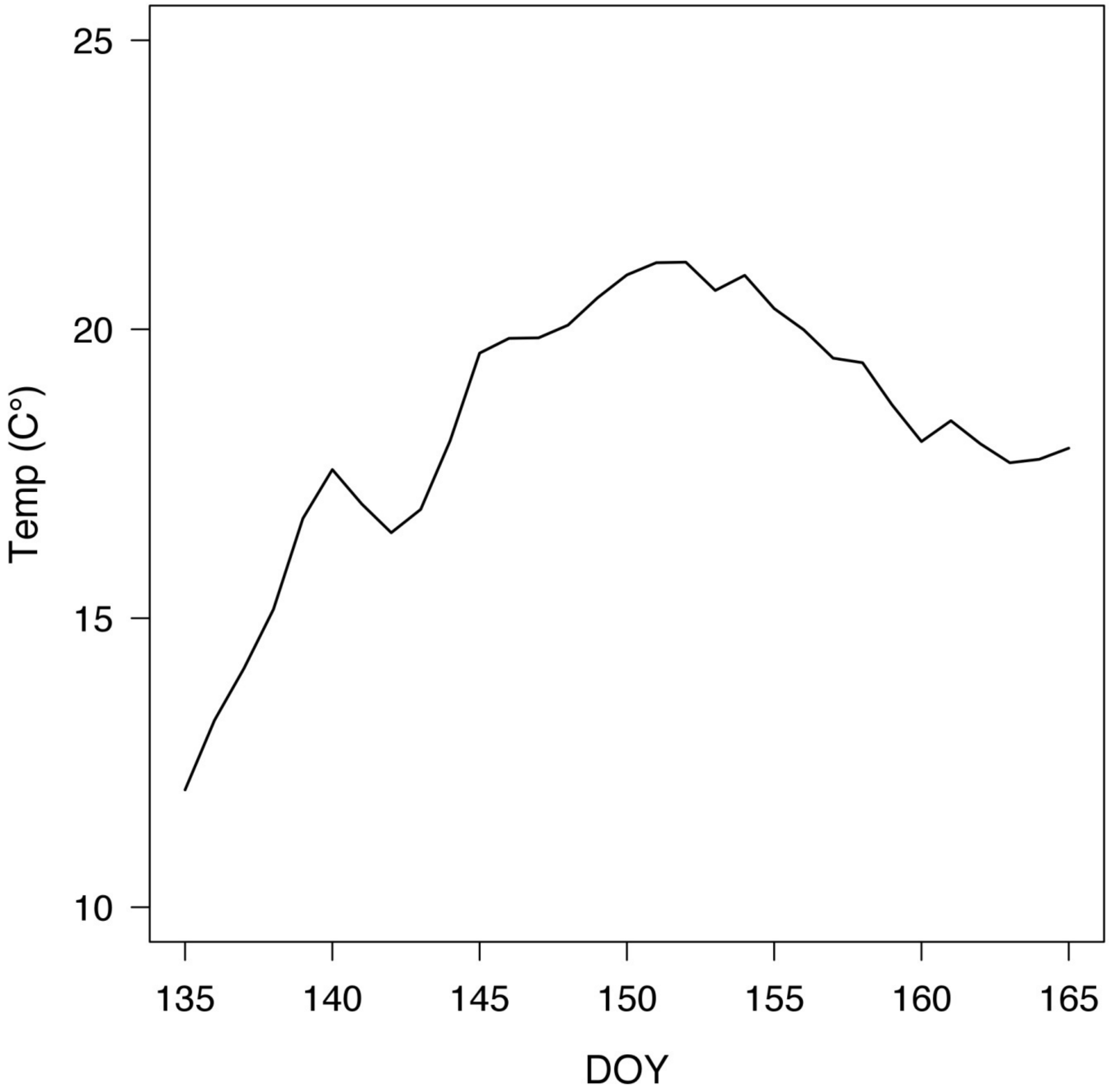

Figure 3 – Mean daily surface water temperature used during bioenergetic simulations. Data were gathered at hourly intervals by an instrumented buoy at the deepest point in Sparkling Lake during the spring of 2010. (http://lter.limnology.wisc.edu/).

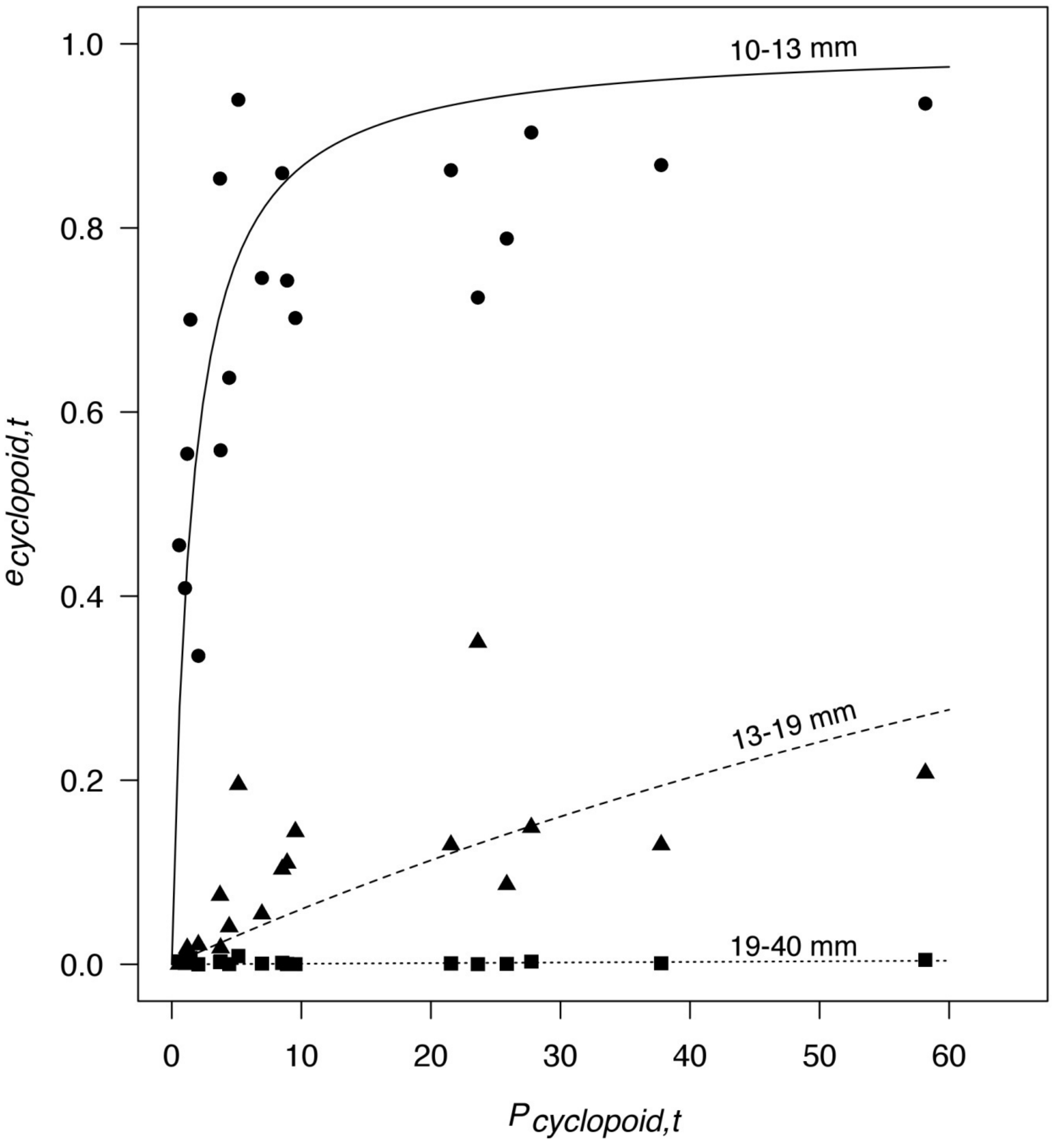

Figure 4 – Above provides an example of estimating the D90 parameters using values of cyclopoid copepods densities collected in all four study lakes during the spring of 2010. Using eq. 12, I estimated values of $e_{cyclopoid,t}$ for each size interval of larval walleye (Table 4) which I was able to relate back to values of $P_{cyclopoid,t}$ using eq. 9. Values of $D90_{\mathrm{cyclopoid,L}}$ were estimated for each size interval. For cyclopoid copepod prey, the values of D90 increases with the larger size classes, indicating cyclopoids are not selected as readily at larger sizes.

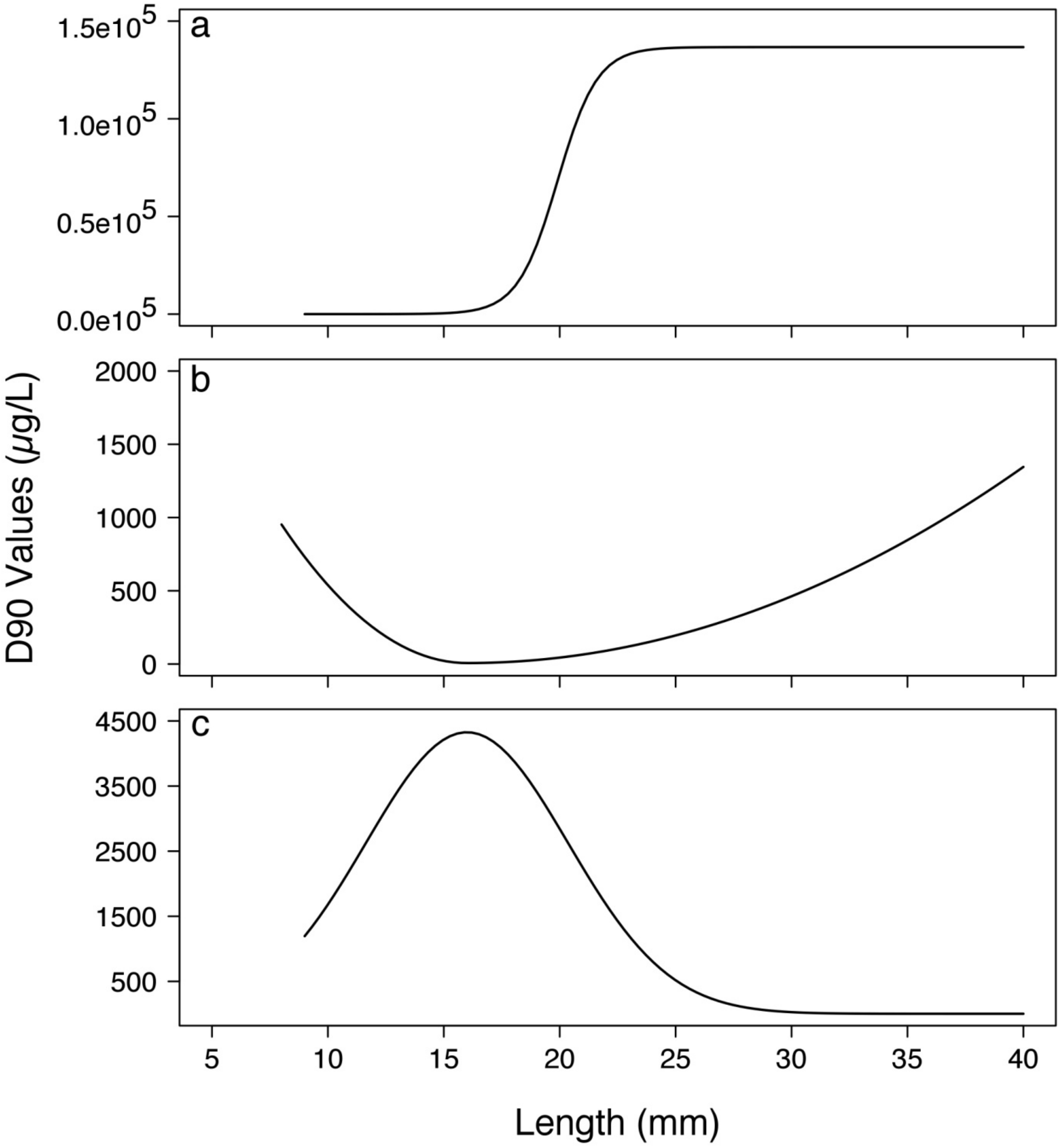

Figure 5 – The derived D90 curves for the three primary diet items of larval walleye (*Sander vitreus*). These curves are based on field observations of larval walleye prey selectivity and prey abundance. (*a*) D90 curve for cyclopoid copepods (eq. 11). (*b*) D90 curve for calanoid copepods (eq. 12). (*c*) D90 curve for *Daphnia* (eq. 13).

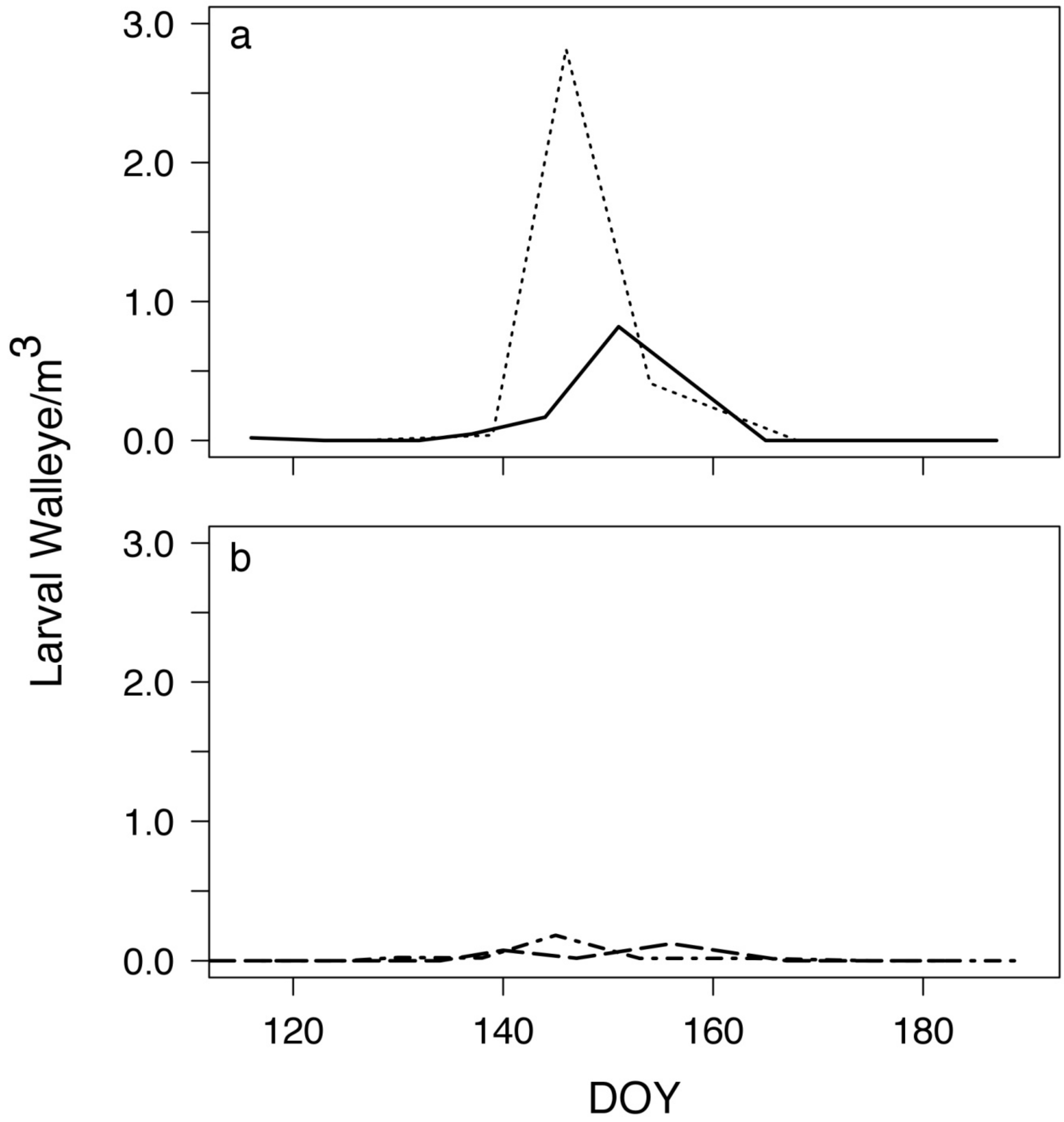

Figure 6 – Total larval walleye (*Sander vitreus*) catches from ichthyoplankton sampling done during the spring of 2011. Densities represent pooled catches from all depths (surface and 1m) and all transects in each lake. (*a*) Larval walleye catches in lakes without rainbow smelt populations: Escanaba Lake (———) and Plum Lake (┈┈┈). (*b*) Larval walleye catches in lakes with rainbow smelt populations: Long Lake (▬ ▬ ▬) and Sparkling Lake (▬ · ▬).

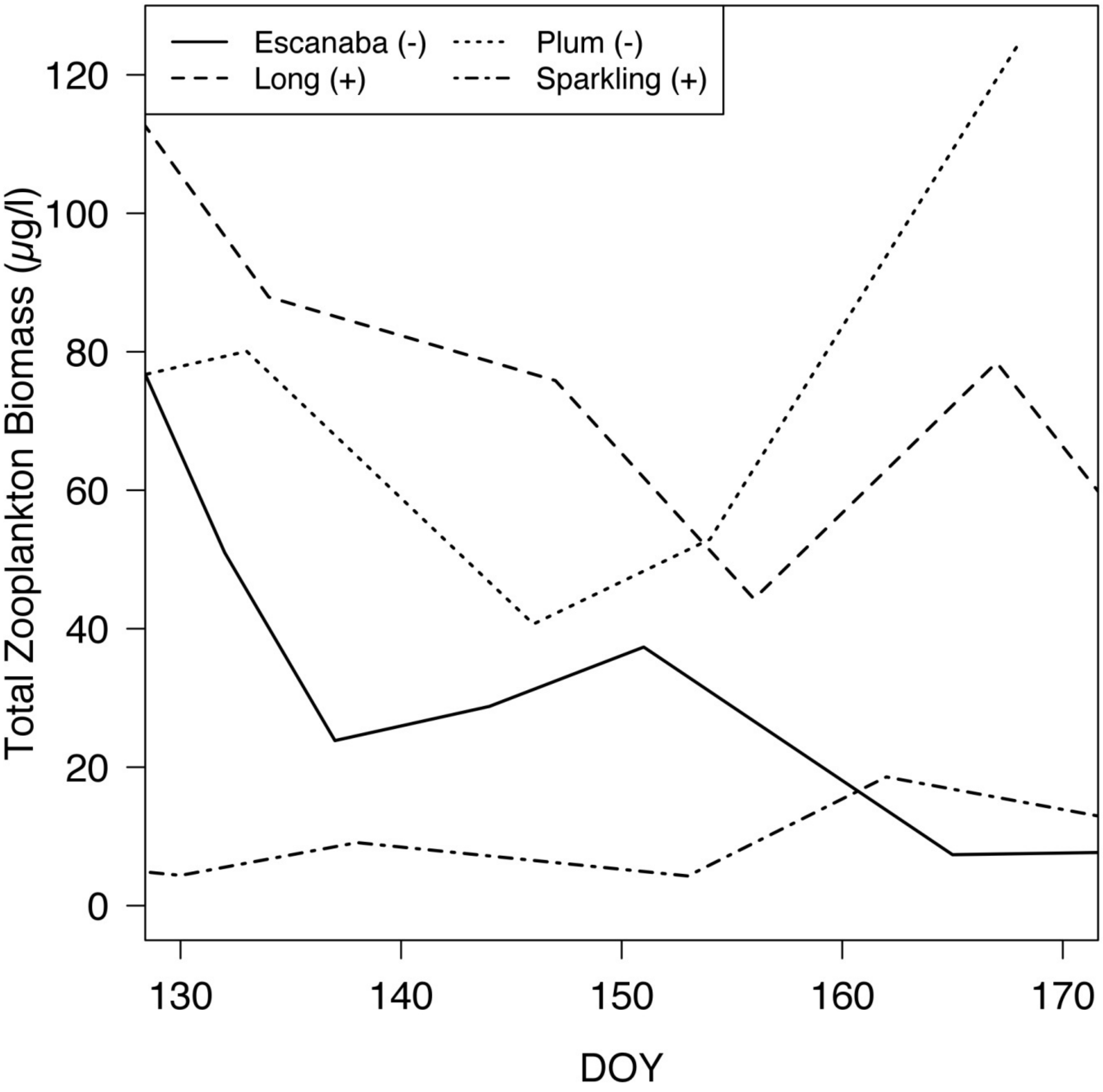

Figure 7 – Total biomass of the pelagic zooplankton community during the spring of 2011. (+) indicates the lakes with rainbow smelt populations and (-) indicates the lakes without rainbow smelt populations.

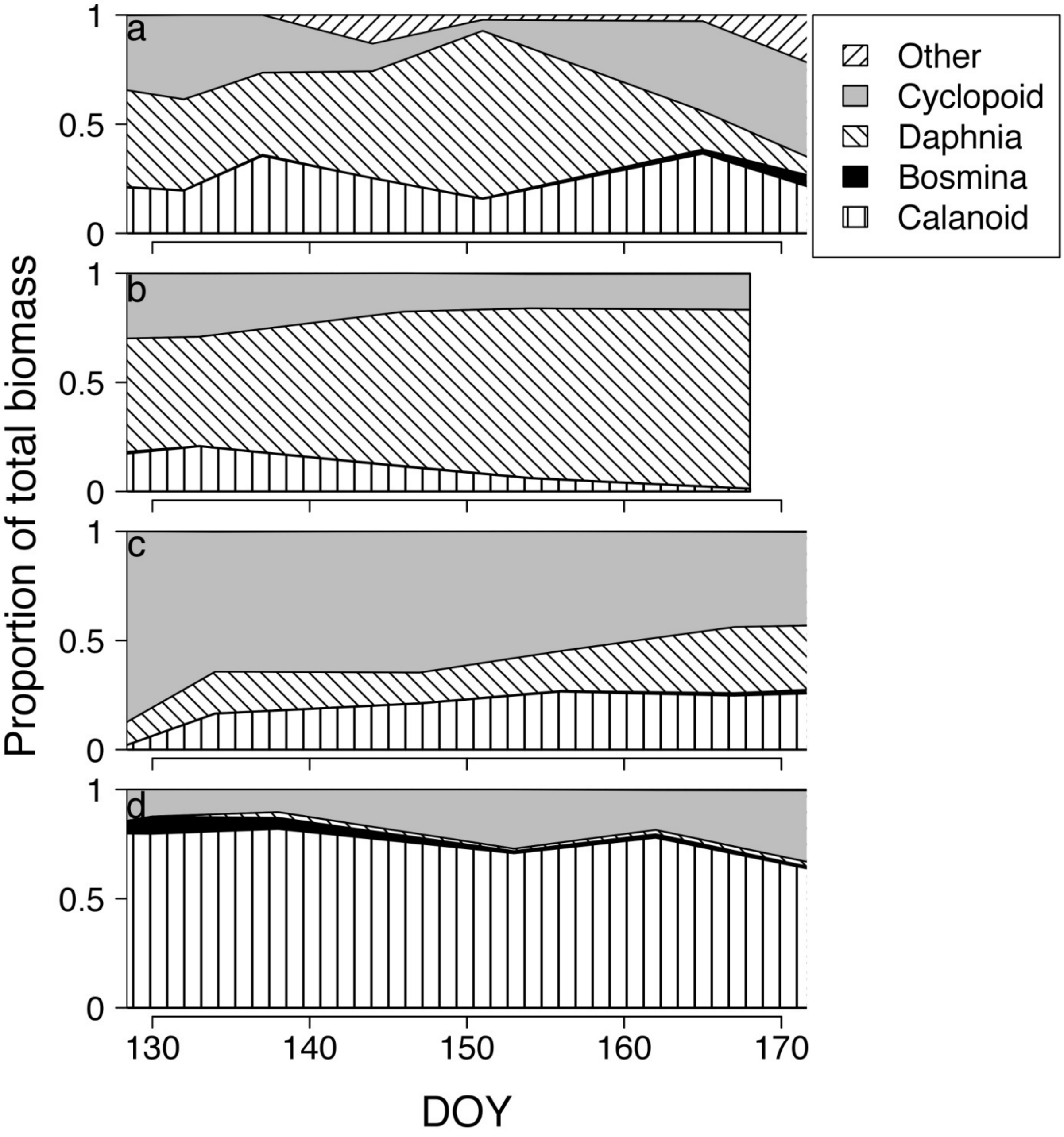

Figure 8 – Zooplankton community composition as proportion of total biomass in all four study lakes. Rainbow smelt were absent in (a) Escanaba Lake and (b) Plum Lake and established in (c) Long Lake and (d) Sparkling Lake.

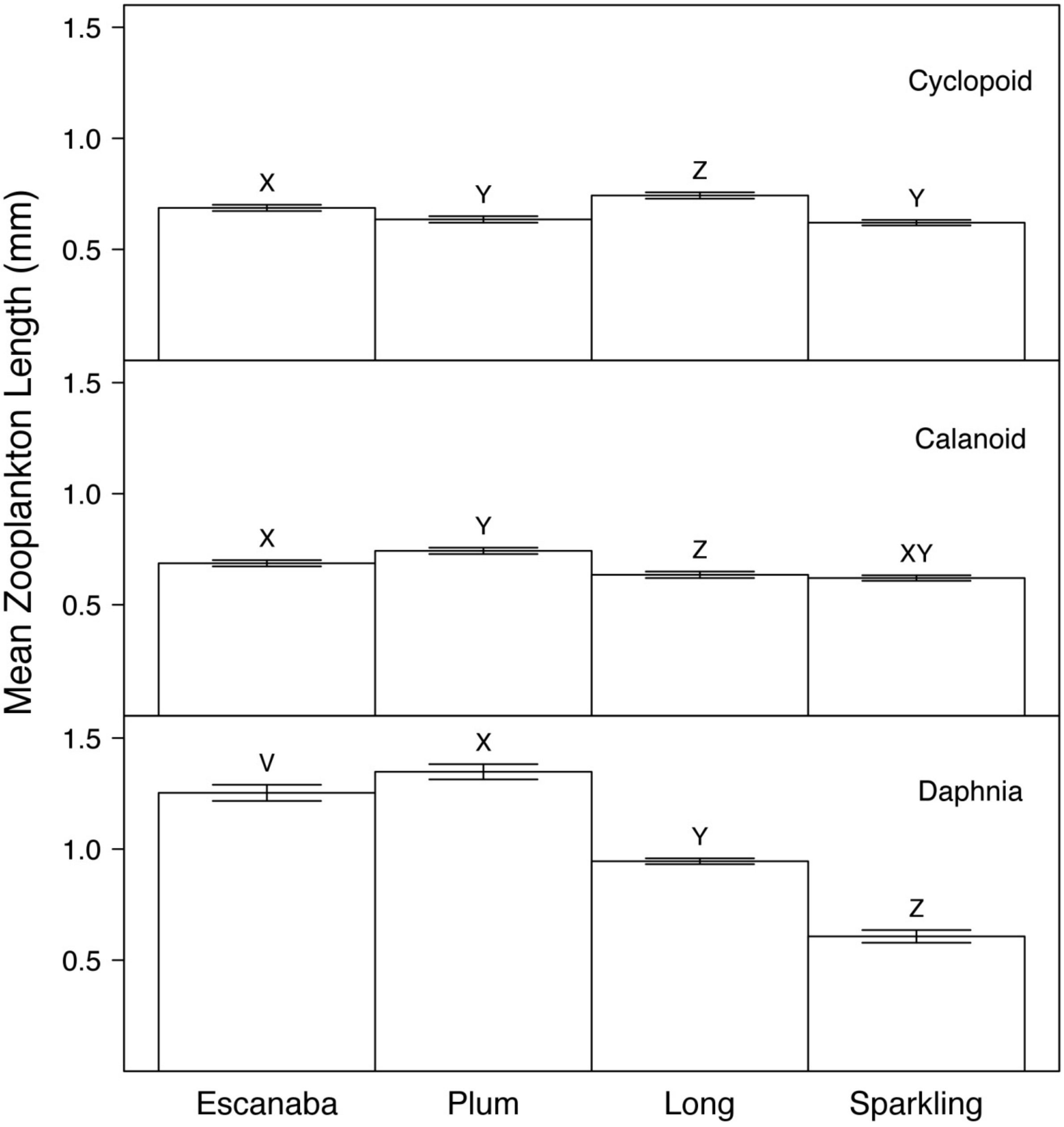

Figure 9 – Mean lengths of cyclopoid copepods, calanoid copepods and *Daphnia* from each study lake, error bars represent ± 1 SE. ANOVA indicated that there were significant differences in length between lakes in each zooplankton category (Cyclopoid – $F_{3,858}$ = 15.336, p = <0.001; Calanoid – $F_{3,814}$ = 20.588, p = <0.001; *Daphnia* – $F_{3,632}$= 65.395, p = <0.001). Values with same letters are not significantly different within each panel (Fishers LSD, P < 0.05).

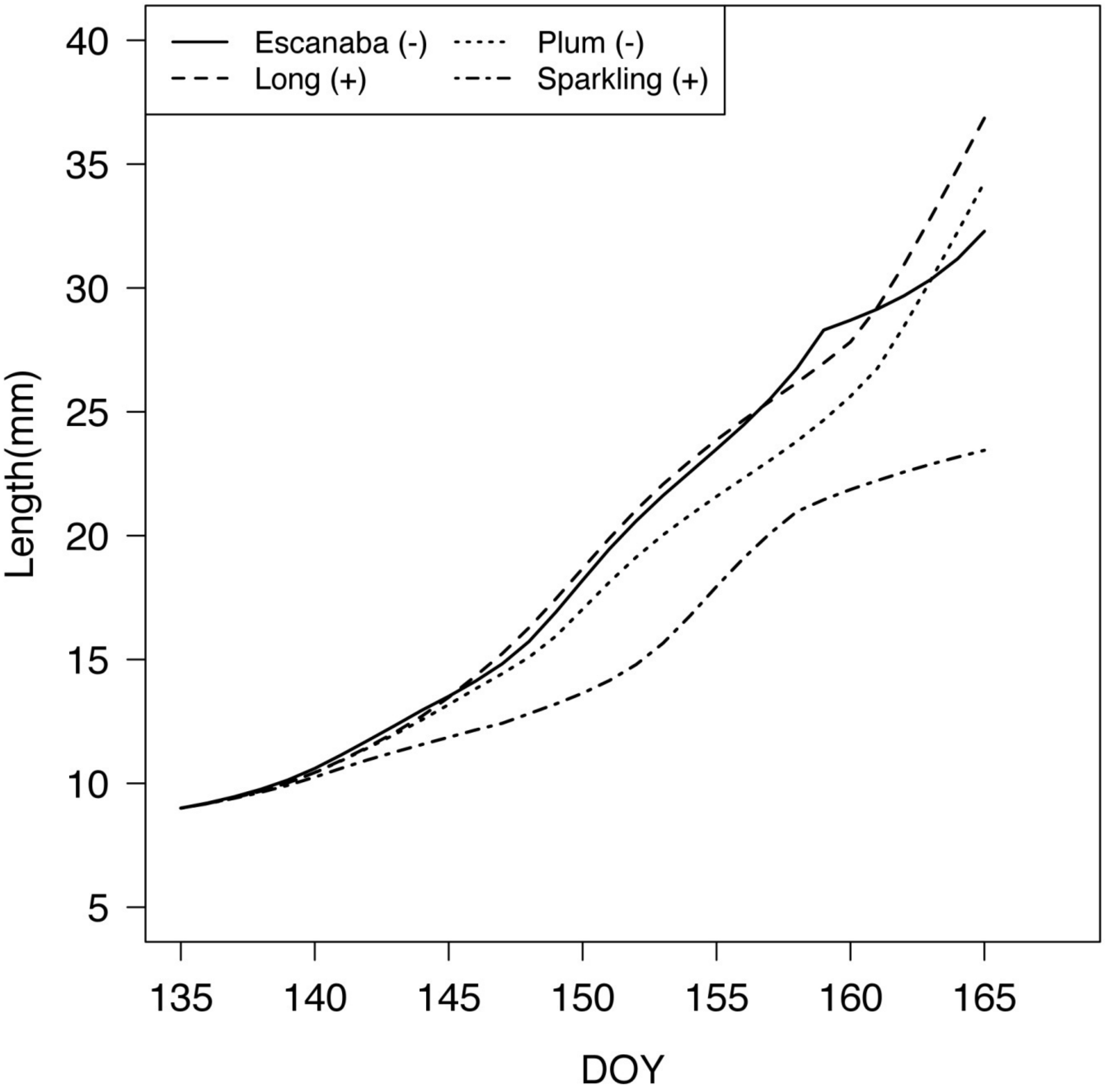

Figure 10 – The Lengths of simulated larval walleye (*Sander vitreus*) in all four lakes modeled after 30 time steps. Only walleye in Sparkling Lake did not attain a length greater than 30 mm. Growth within the other three lakes was relatively similar.

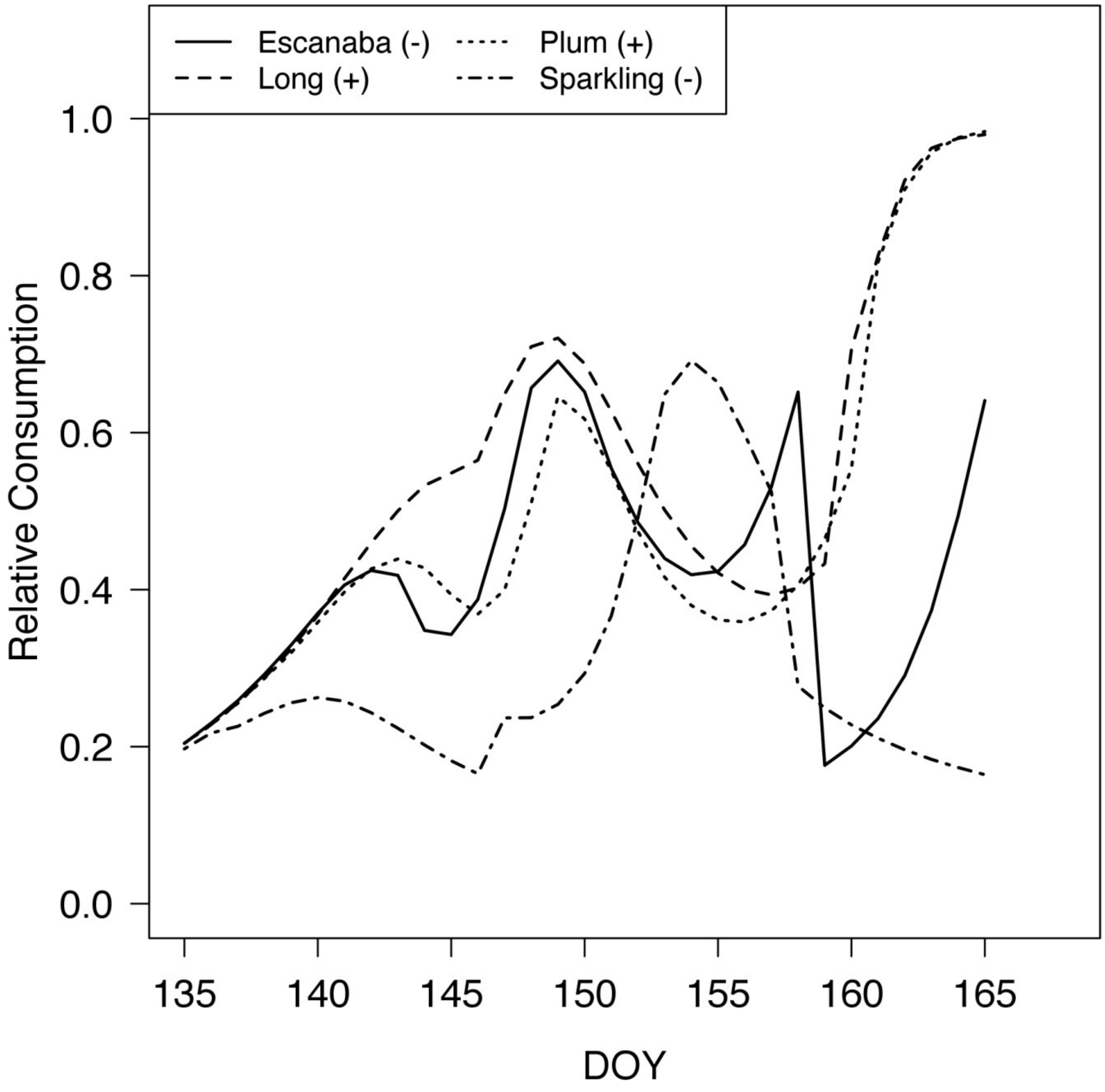

Figure 11 – P-values of simulated larval walleye (*Sander vitreus*) over 30 simulated days. The p-value represents the consumption of the larval walleye as proportion of their C_{max}.

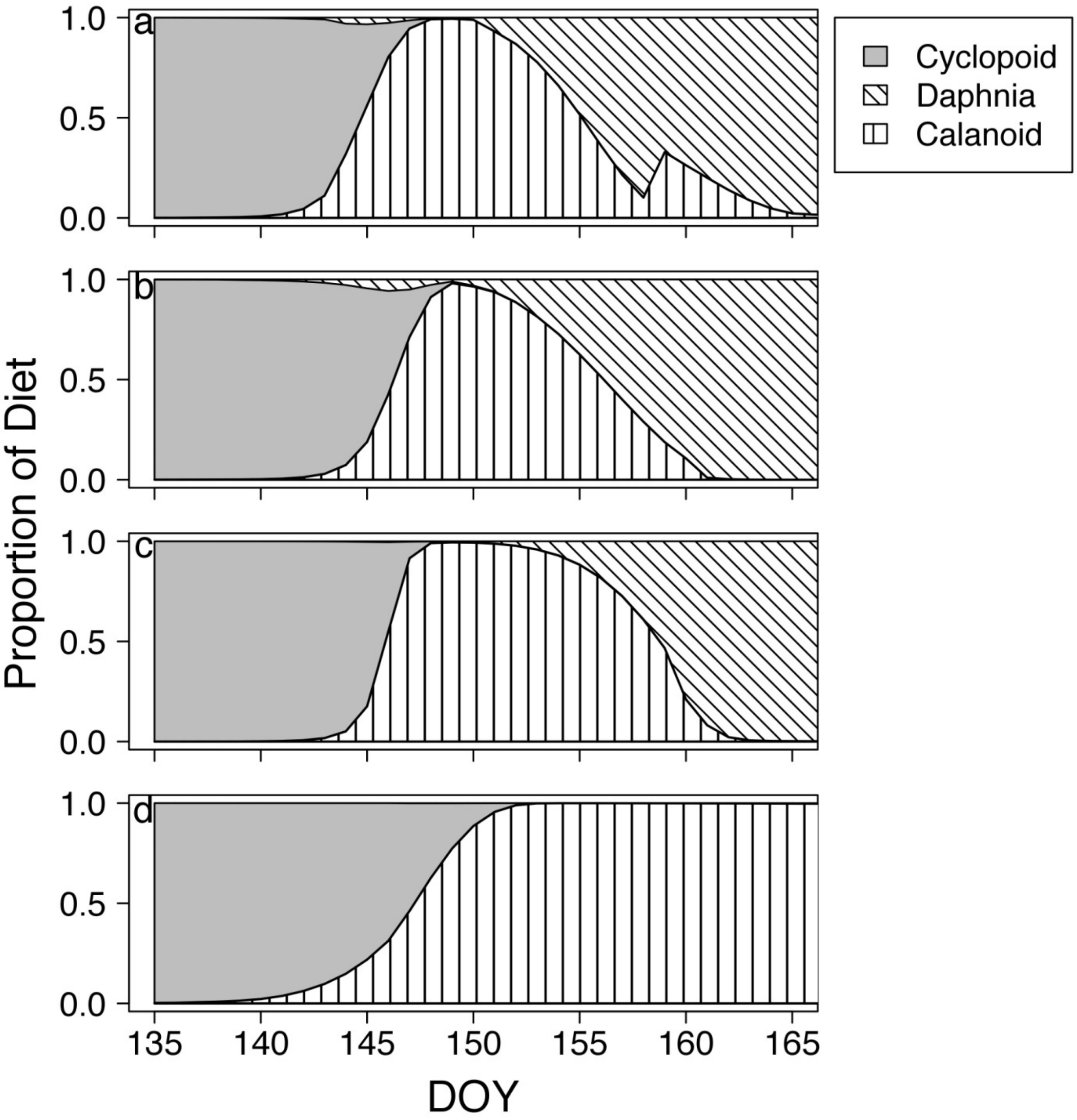

Figure 12 – Diet proportion of the simulated larval walleye (*Sander vitreus*) in all four lakes: (*a*) Escanaba, (*b*) Long, (*c*) Plum and (*d*) Sparkling. All three prey types were consumed in each lake except Sparkling Lake. In Sparkling Lake the larvae did not reach lengths large enough for *Daphnia* to become an important part of their diet.

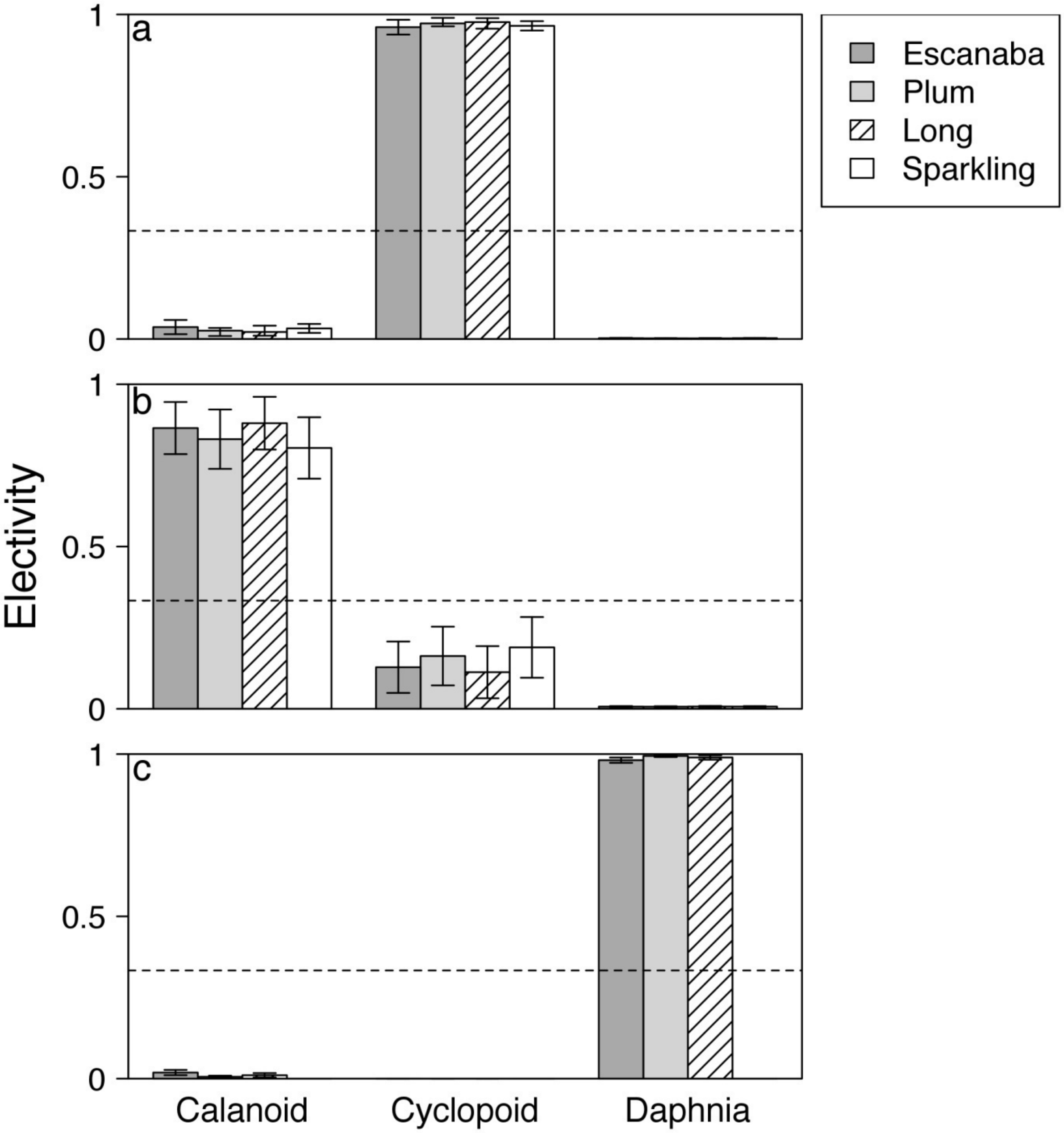

Figure 13 – The selectivity (Manly's β) of the three size classes of larval walleye (*Sander vitreus*) modeled: (*a*) 8-13 mm, (*b*) 13-19 mm and (*c*) 20-39 mm. The horizontal line represents neutral selection.

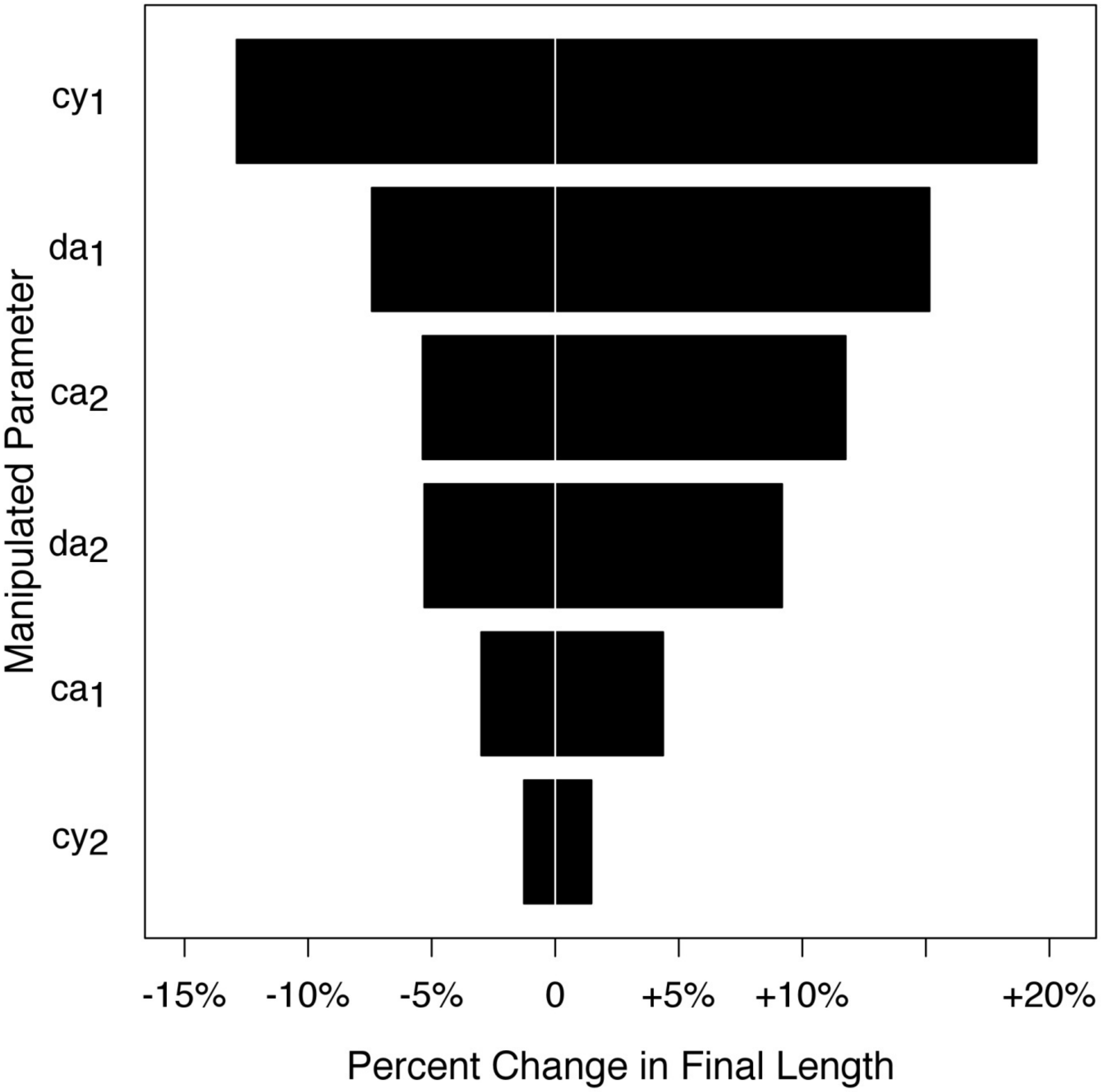

Figure 14 – A tornado diagram displaying the results from the sensitivity analysis. The diagram shows how final modeled larval walleye length varied during the parameter manipulation, with the most sensitive parameter at the top and the least sensitive parameter at the bottom. The model was sensitive to three parameters: ca1, cy2, and da2, all of which saw a greater than ±10% change in final length after a manipulation of ±10% the original parameter value.

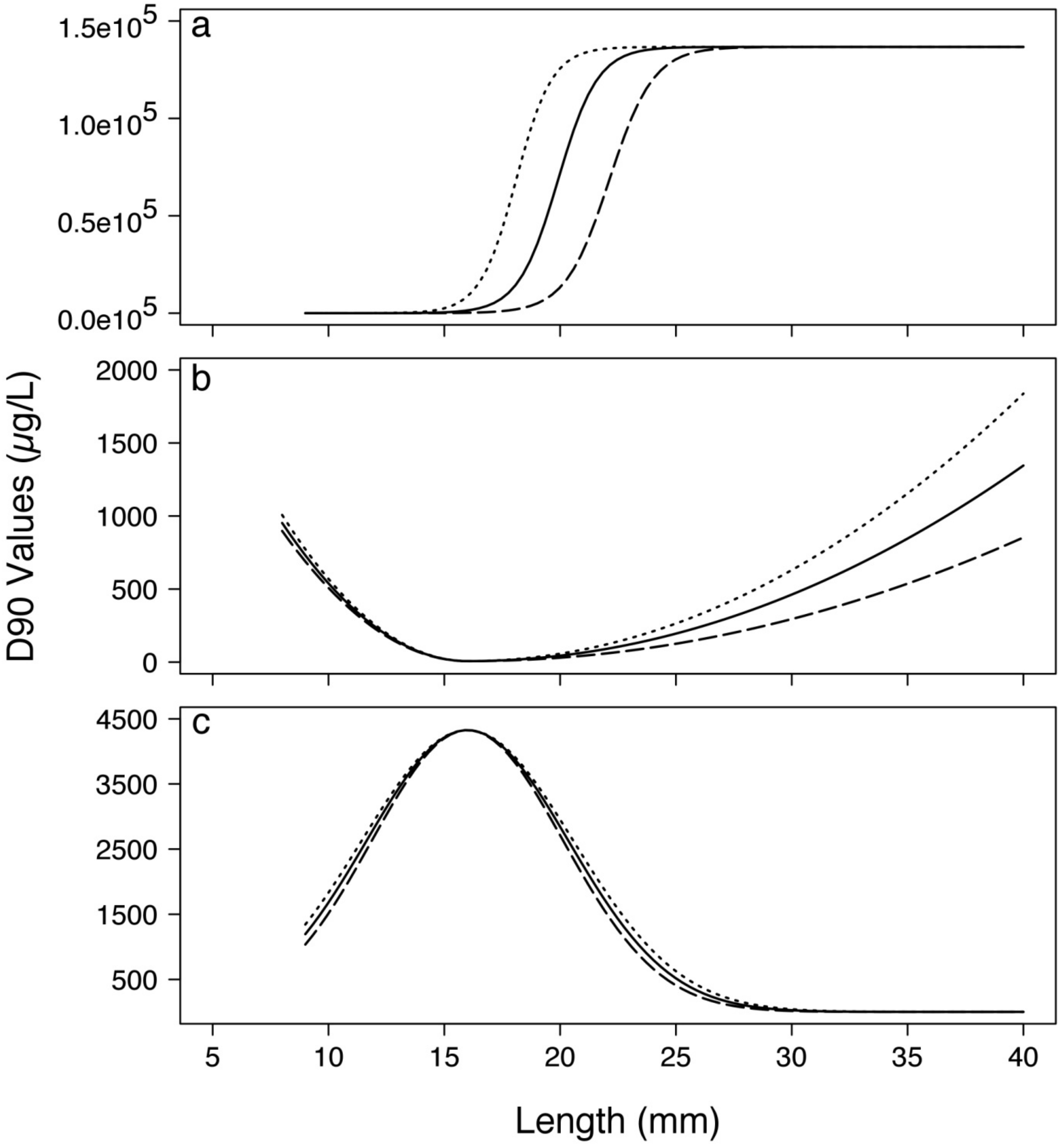

Figure 15 – In each plot a parameter that the model was sensitive to is altered by ±10%: (a)cy2in eq. 12, (b) ca1 in eq. 11, and (c) da2in eq. 13. All three parameters control the rate of change within their respective curves. In each plot the dashed line (— — —) represents the -10% parameter manipulation and the dottled line (········) represents the +10% parameter manipulation.

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