ASSESSMENT OF THE EFFECTS OF HABITAT, HARVEST AND COMMUNITY INTERACTIONS ON THE ABUNDANCE OF WALLEYE *SANDER VITREUS* IN INLAND LAKES THROUGHOUT ONTARIO

by

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A thesis submitted to the Department of Biology
In conformity with the requirements for
the degree of Master of Science

Queen's University
Kingston, Ontario, Canada
September, 2012

Abstract

Walleye (*Sander vitreus*) is an important species to the recreational fishery throughout Ontario. Fish community interactions between walleye and other species are rarely considered when establishing management targets which may lead to the creation of conflicting management objectives. Other studies that have focused on competitive interactions between species have typically focused on interactions between two species in isolation of the remaining species within the fish community and considered only a small subset of lakes. My study examined how the presence/absence of multiple species within the fish community affects the abundance of walleye across a broad spectrum of habitat conditions and fisheries. A Schaefer model was modified by distinguishing carrying capacity into a habitat and fish community component to account for between lake differences in suitable habitat prior to testing for interactions. Walleye catch-per-unit effort (CUEW, kg/net) was assessed in 140 Ontario lakes using the Fall Walleye Index Netting Protocol. An all subsets approach was used to estimate parameters in a multiple regression. Fish community and fishing pressure were significant predictors in explaining walleye abundance (adjusted R^2=0.45, $p<0.001$). The presence of bluegill (*Lepomis macrochirus*) and smallmouth bass (*Micropterus dolomeiu*) were significant negative predictors in the top model ($\alpha_{bluegill} = -1.54$, partial r^2=0.1; $\alpha_{smallmouth} = -0.28$, partial r^2=0.03). In many studies, smallmouth bass have also been found to have a significant diet overlap with walleye. These interactions present challenges when establishing management objectives for mixed fisheries.

Acknowledgements

I would like to begin by thanking my supervisor, Dr. Bruce Tufts for providing me with the opportunity to pursue graduate research and ongoing support and guidance throughout my degree. His confidence in my abilities afforded me a unique opportunity to be involved in a diversity of experiences that would otherwise not have been possible. I would like to thank the additional members of my supervisory committee, Dr. Nigel Lester and Dr. John Casselman for their encouragement and holding me accountable to their exceptional standards.

I would like to thank Dave Brown and Chris Robinson for providing mentorship and opportunities in the early part of my career that eventually put me in a position to be able to pursue graduate research.

This project was funded through a partnership with the Ontario Ministry of Natural Resources (OMNR) and the Freshwater Fisheries Fund at Queen’s University. I am grateful to all of the field staff of the OMNR and the Cooperative Freshwater Ecology Unit, Laurentian University that contributed to the collection and management of an extensive database of projects upon which my analysis was conducted. I would also like to acknowledge the financial support of Shimano Canada, the Ontario Federation of Anglers and Hunters, the Canadian National Sportsmen’s Shows and the Canadian Sportfishing Industry Association through their contributions to the Freshwater Fisheries Fund at Queen’s University.

I am indebted to the extensive support from my in-laws. To my siblings, whom I don’t see nearly enough, thank you Robin for providing observations from the water to remind me of the importance of this work and to Becky for always being able to provide the appropriate amount of encouragement and motivation. My parents instilled in me at an early age a love for fishing and too many lessons to list and I can’t thank them enough. Finally, to Beth, my best friend and life partner, thank you for your unconditional love, support and sacrifice every day throughout this process.

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List of Abbreviations

Abbreviation	Full Name
AHI	Aquatic Habitat Inventory
BRP	Biological Reference Point
BSM	Broadscale Monitoring Program
CUEW	Catch as Biomass per Unit Effort (kg/net)
DFO	Fisheries and Oceans Canada
FLEN	Fork Length (mm)
FMP	Fisheries Management Plan
FMZ	Fisheries Management Zone
FWIN	Fall Walleye Index Netting
GDD	Growing Degree Day
IGP	Intraguild Predation
LPP	Ministry of the Environment Lake Partner Program
MDS	Multidimensional Scaling
MSY	Maximum Sustained Yield (kg/ha)
OMNR	Ontario Ministry of Natural Resources
OMOE	Ontario Ministry of the Environment
RWT	Round Weight (g)
TDS	Total Dissolved Solids
TOHA	Thermal Optical Habitat Area
TOHAI	TOHA Index (TOHA/Area)

Chapter 1

General Introduction

Recreational fishing in Canada provides important cultural, recreational and economic benefits to residents and tourists. In Ontario, the recreational fishery contributes over $2 billion in expenditures to local economies (Fisheries and Oceans Canada 2007). Despite the economic importance of recreational fisheries, anglers do not benefit from the direct economic incentives in the same manner that drive commercial fisheries which have seen widespread collapse throughout the 20th century (Post *et al.* 2002). Management of recreational fisheries benefits from many concepts developed from commercial fisheries however recreational fisheries differ in that there may be less emphasis placed on maximizing yield from a fishery in favour of managing for angler satisfaction (Radomski 2003). Biological reference points (BRPs) are one management tool adopted from commercial fisheries. BRPs denote thresholds or indices regarding stock size that may trigger management actions, such as the reduction of creel limits if the stock size approaches the BRP (Isermann and Paukert 2010). Marine fisheries use extensive catch data to develop BRPs. Recreational fisheries on inland lakes typically do not have the advantage of long term data to establish BRPs. Another challenge is that conditions vary between lakes making comparisons of reference points difficult. Physical attributes, such as total dissolved solids, have been used to develop models guiding safe harvest rates between lakes (e.g. Ryder 1965, Lester *et al.* 2004) however one limitation of these models is that fish community effects are not taken into account. This thesis attempts to quantify how different fish communities can affect the BRPs of lakes.

Species interactions underlie many of the processes in fisheries. Tonn (1990) illustrates how fish communities are formed through a series of environmental and fish community interactions acting as a series of filters that ultimately define community diversity across a landscape. Human intervention can, and regularly does, by-pass historical filters through the introduction (intentionally or otherwise) of non-native species. There is a growing trend in marine fisheries towards a multispecies, ecosystem based approach (Mace 2001, Link 2002). In contrast freshwater fisheries management plans still tend to focus on single species targets, perhaps within broader goals for ecosystem integrity (Kwak and Freeman 2010). Walters and Kitchell (2001) cite the complexity of ecosystem approaches as a barrier to implementation in management but suggest that constructing collections of individual based models can provide an ecosystem approach to management with reliability that is comparable to the single species analogues.

Establishing appropriate BRPs for multiple species requires an understanding of each species' niche. Hutchison (1957) introduced the concept of a multidimensional niche which is composed of a fundamental and realized niche. The fundamental niche is based on biotic and abiotic factors. The realized niche will be a reduced subset of the fundamental niche as a result of species interactions such as sharing and competitive exclusion. A great deal of effort has been devoted to understanding the abiotic component of a species' niche (Orth 1983, Pegg and Chick 2010) which has led to an extensive understanding of habitat requirements for many recreationally important fish species (Scott and Crossman 1979, Edwards *et al.* 1983, McMahon *et al.* 1984, Christie and Regier 1988). Interpretation of stock status within a waterbody should consider the constraints imposed by the available niche. Variation in stock abundance or biomass between lakes should vary across a landscape in proportion to the amount of variation in suitable habitat between lakes. This habitat variation between lakes can present challenges for establishing broad BRPs or interpreting stock status.

A species' realized niche can differ among and within a lake depending on the plasticity of the species and interspecific competition for resources. *Coregonis* spp. show great diversity in their realized niche and include planktivores (subgenus *Leucichthys*), benthivores (subgenus *Coregonus*) and piscivores (genera *Stenodus*) (Lindsey 1981). Lake Superior has seven sympatric coregonid species filling specialized niches (Lindsey 1981). The realized niche of a species may change in response to the presence or absence of another species with an overlapping niche. Robinson *et al.* (2000) showed how the niche of pumpkinseed (*Lepomis gibbosus*) contracts or expands based on the presence and absence, respectively, of bluegill (*L. macrochirus*). Juvenile competition between pumpkinseed and bluegill may cause pumpkinseed to specialize their diet on snails rather than a more diverse littoral diet (Osenburg *et al.* 1992).

Interactions between two species can be described by 7 categories (Table 1, Tyus 2012). Competition and predation will be the focus of this research. Competition between two species is often difficult to quantify as the nature of the competition may differ seasonally, between lifestages or only at times of limited resources (Tyus 2012). With regard to predation, the relationship between two species may also change over time. For example, the prey may eventually grow beyond a vulnerable stage and reach a size where it becomes the predator.

Intraguild predation (IGP) is broadly defined by Polis *et al.* (1989) to include all taxa in a community that may compete for resources. Mutual predation (Symmetrical IGP) between two species is often observed in an age structured manner. For example, juveniles of species "A" may be initially preyed upon by species "B" but following an ontogenetic shift to piscivorey, species "A" can become a predator of species "B". This "trophic triangle", "competitive bottleneck" or “predator-prey reversal” can result in several possible equilibriums between the two populations due to depensatory effects that can prevent the rebuilding of a sizeable predator base to limit the impacts of juvenile predation (Walters and Kitchell 2001).

Exploitative competition occurs between two species where there is competition for resources, often in the form of diet overlap (Tyus 2012). Diet overlap, however, may only rarely result in interspecific exploitative competition when food resources are limiting as it is common for species’ diets to overlap, especially when prey is abundant (Matthews 1998). Two or more species within a fish community can coexist at the same tropic level with similar resource requirements through equalizing or stabilizing mechanisms that result in a stable coexistence (Chesson 2000). Ruan *et al.* (2007) demonstrate that density dependent mortality is necessary for two competitors to coexist on a single prey item. Cushing and Li (1991) conducted model analyses and determined that increased competition resulted in a lower population abundance at equilibrium. It is expected that populations undergoing competitive interactions will have a lower abundance than expected based on available habitat.

Table 1. Types of species interactions adapted from Tyus (2012). "+" indicates a positive effect for the species (S1 or S2), "-" is a negative effect and "0" is no effect.

Interaction	S1	S2
Mutualism	+	+
Competition	-	-
Predation	+	-
Parasitism	+	-
Commensalism	+	0
Amensalism	-	0
Neutralism	0	0

Chapter 2

Introduction

Walleye (*Sander vitreous*) is a popular game species that has a natural and introduced range spanning most of Canada and the United States (Billington *et al.* 2011). Walleye is one of the most targeted species in Ontario's recreational fishery (Ontario Ministry of Natural Resources (OMNR) 2009) known to occur in more than 4000 lakes and 800 rivers in the province (OMNR 1987, MacLeod and Wiltshire 2004). This important resource is managed in Ontario largely through the use of fisheries management plans (FMPs) that set targets for species abundance and recommend harvest controls (e.g. creel, size and gear limits) in order to meet those targets.

A single species approach to target setting may inadvertently establish contradictory management goals that result in excessive predation or depensatory effects on one or more of the target species, impairing the ability to achieve management objectives. Modeling results suggest that when exploitation and community interactions occur, equilibrium biomasses will be lower (Gamble and Link 2009). The nature of the fish community will also be important to consider when assessing the viability of introducing or supplementing walleye through stocking (Fayram *et al.* 2005, Kerr *et al.* 1996). It follows that assessing the strength of interactions between walleye and other species is important in establishing realistic management goals where the potential for species interactions exist (Fayram *et al.* 2005). Baccante and Colby (1996) provide a broadscale analysis indicating that population size, habitat and fish community are important to consider when establishing harvest rates but their analysis did not specifically assess community factors. Although significant progress has been made in terms of our understanding of how habitat (Ryder 1977, Lester *et al.* 2004, Bozek *et al.* 2011a), climate (Zhao *et al.* 2008, Venturelli *et al.* 2010, Bozek *et al.* 2011b) and recruitment dynamics (Busch *et al.* 1975, Colby and Nepszy 1981, Baccante and Reid 1988, Barton and Barry 2011) affect fish biomass, species interactions are often difficult to assess (Tyus 2012, Knapp *et al.* 2012).

Even in simple, well understood predator-prey relationships, there is potential to establish conflicting management objectives. Rudstam *et al.* (1996) highlighted the potential for conflict in management objectives through an investigation of walleye and yellow perch (*Perca flavescens*) dynamics. Yellow perch are an important prey item for walleye and it was determined that growth rates of the two species are negatively correlated. Management objectives established on two study lakes were intended to increase perch growth. This would provide larger perch for the recreational fishery. This objective was initially welcomed until walleye growth rates declined. As systems and interactions become more complex the likelihood of creating conflicting management objectives is likely to increase.

Many centrarchid species are native to Ontario although species ranges have expanded through deliberate introductions and invasive pathways. Understanding the extent that intraguild predation and exploitative competition exists between walleye and members of the centrarchid family is important to fisheries management. Smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*M. salmoides*) were widely introduced throughout Ontario during the latter part of the 19th and early part of the 20th centuries (Lasenby and Kerr 2000). Widespread introductions such as these were common practice at the time and occurred in many jurisdictions with little consideration towards community impacts (Jackson 2002). The range of smallmouth bass has also been increasing over the past century (Dunlop and Shuter 2006). Models predict that a climate increase of 2°C would further increase smallmouth bass ranges throughout North America (Chu *et al.* 2005). Conversely, increasing temperatures could mean reduced reproductive success for walleye in some of the more southern populations (Meisner *et al.* 1987). Vander Zanden *et al.* (2004) modeled the invasion threat of smallmouth bass into lake trout (*Salvelinus namaycush*) lakes and suggested that a similar analysis be conducted to assess impact of other littoral predators.

Smallmouth and largemouth bass are growing in popularity in recreational fisheries and regulations across jurisdictions are increasing in complexity to maintain quality fisheries (Noble 2002). Competitive bass (both smallmouth and largemouth sp.) fishing events continue to increase in Ontario. In 2008, Ontario had 481 competitive bass fishing events (Kerr 2009), up from 249 in 1998 (Kerr 1999) although the proportion relative to all competitive fishing events remained similar (35.5% and 37.4%, respectively). The proportion of fish retained (# harvested/# caught x 100) in Ontario recreational fisheries for smallmouth (12.3%) and largemouth (12.2%) is marginally lower than for walleye (18.3%) and it is estimated that more than five times the number walleye are harvested annually compared to smallmouth bass (OMNR 2009). Other centrarchid species such as black crappie (*Pomoxis nigromaculatus*) and bluegills (*Lepomis macrochirus*) are important components of the Ontario fishery and their range also continues to expand from intentional and unintentional introductions.

Centrachid species may affect walleye populations through direct predation on walleye or through exploitative competition. Juvenile centrarchids have been identified as a significant source of mortality on stocked walleye (Hoxmeier *et al.* 2006). Brooks *et al.* (2002) suggested that the abundance of largemouth bass could be one reason that walleye stocking efforts were unsuccessful in producing walleye fisheries in some Illinois lakes. Predator (bluegill and yellow perch) abundance was also found to be negatively correlated with survival of stocked walleye in Lake Mendota, Wisconsin (Johnson *et al.* 1996). According to Seip (1995), high abundance of walleye, perch, black crappie, and largemouth bass hindered the success of stocked walleye in Ontario lakes. In an Iowa lake where largemouth bass and walleye coexist, it was determined that juvenile walleye make up as much as 16% of the diet of largemouth bass (Liao *et al.* 2004). High predation rates on stocked walleye may result from strong habitat overlap between largemouth bass and age-0 walleye (Pratt and Fox 2001). Controlled laboratory experiments also showed that largemouth bass are highly successful at capturing walleye in simulated vegetation (Wahl 1995). High predation rates on juvenile walleye may be the underlying mechanism for the strong negative relationship between walleye and largemouth bass abundance found in Wisconsin lakes (Nate *et al.* 2003).

It is important to consider that direct predation of juvenile walleye does not necessarily limit walleye recruitment. The extent to which predation affects recruitment depends on compensation processes (Jensen 1992). Many fish are general predators eating prey in proportion to their abundance and provide a stabilizing effect by reducing intraspecific competition (Bax 1998). Walleye cannibalism has been shown to be a significant source of mortality in several walleye populations (Chevalier 1973, Mills and Forney 1988, Johnson *et al.* 1992, Kocovsky and Carline 2001). Predation on walleye fry by other species may reduce intraspecific competition and have little overall impact on annual recruitment. In order for predation to have a significant competitive effect, predation must lead to a reduced walleye biomass.

Examples of smallmouth bass acting as a predator on juvenile walleye are not as consistent compared to largemouth bass. Johnson and Hale (1977) found that walleye made up a small percentage of smallmouth bass diets but did observe a decrease in walleye recruitment as smallmouth bass increased in three of four study lakes. Frey *et al.* (2003) also found no evidence of walleye in smallmouth bass diets in a Wisconsin lake. In contrast, Zimmerman (1999) analyzed almost 1000 smallmouth bass stomachs and did not find a single walleye. According to Liao *et al.* (2004) however, smallmouth bass do use walleye as a significant diet item in Spirit Lake, Iowa.

Other centrarchids have also been shown to prey on walleye fry and cause declines in walleye abundance. White crappie (*Pomoxis annularis*) abundance has been shown to have a significant negative effect on walleye recruitment (Quist *et al.* 2003a). Schiavone (1985) attributed the collapse of the walleye fishery in the Indian River Lakes, New York, to the introduction of black crappie. High densities (>50kg/ha) of bluegill were also correlated with walleye year-class failures and associated lab studies confirmed that bluegill could utilize walleye fry as prey (Schneider 1997).

Post *et al.* (2002) predict declines in production as depensatory mechanisms increase. If predation was a limiting factor, a lower equilibrium biomass may be expected in systems where juvenile predation is significant. Fruetel (1995) observed a negative association between walleye and smallmouth bass year classes. Robilliard and Fox (2006) attributed a consistent decline in walleye abundance in the Kawartha Lakes to environmental factors and competitive interactions with *Micropterus* spp. Fayram *et al.* (2005) found that largemouth (but not smallmouth) bass abundance was negatively correlated with walleye abundance in a survey of 20 Wisconsin Lakes. In a 30 year investigation of Oneida Lake, Hall and Rudstam (1999) did not observe a significant correlation between walleye and smallmouth bass or pumpkinseed abundances. Although there is evidence that walleye abundance may be limited by *Micropterus* spp., lake variability may play a role in determining the significance of the relationship. It must also be acknowledged that walleye recruitment is highly variable from year to year and is often directly related to environmental conditions (Hansen *et al.* 1998, Mion *et al.* 1998, Schupp 2002), habitat changes (Hoyle *et al.* 2008) or prey abundance (Quist *et al.* 2003b, Madenjian *et al.* 2006).

Direct predation may also be mitigated when walleye are in sufficient abundance to maintain fry predators at levels that prevent depensatory efforts. Walleye have been introduced in high density to water bodies with small sized centrarchid populations with the intent that predation by walleye would reduce centrarchid abundance to levels where centrarchid growth rates and body size would increase. Even at low walleye densities (<0.5 walleye/acre), bluegill growth characteristics increased as a delayed response to walleye stocking and provided a more desirable fishery in Michigan lakes (Schneider and Lockwood 2002). Kolar *et al.* (2003) found that walleye grew well when foraging in bluegill-dominated systems and that a high abundance of bluegill could mitigate growth differences when gizzard shad, the preferred prey, were in low abundance. Walleye preferred gizzard shad however as a diet item over bluegill in tank experiments (Einfalt and Wahl 1997). Growth rates of black crappies have also been shown to increase significantly following the introduction of saugeye (walleye × sauger (*Sander canadense*) hybrids) (Galinat *et al.* 2002).

Diet overlap between walleye and centrarchid species may lead to exploitative competition. Walleye become piscivorous at a relatively small size if suitable prey species exist (Chipps and Graeb 2011). Mittlebach and Persson (1998) suggest that a walleye's diet will be greater than 90 percent piscivorous but actual prey species are highly variable and reflect the regional distribution and availability of prey species**.** Even as an introduced species in a fish community with an existing diversity of piscivores, walleye were able to maintain a piscovorous diet (Liao *et al.* 2004).

Laboratory studies have shown that smallmouth bass can out-compete walleye for prey (Wuellner *et al.* 2011a). Diet overlap between walleye and smallmouth bass was high in systems where gizzard shad (*Dorosoma cepedianum*) was the dominant forage item, however, the competitive interaction was mitigated by the fact that the availability of prey did not appear to be limiting to either species (Wuellner *et al.* 2010, Wuellner *et al.* 2011b). In the lower Columbia and Snake Rivers, Oregon, where both walleye and smallmouth bass have been introduced, these species have been shown to have a high overlap in diets (Zimmerman 1999). Juvenile walleye and smallmouth bass diets were found to overlap in one study lake, but differed significantly in the three other Minnesota study lakes (Johnson and Hale 1977). Where diets differed, crayfish were an important prey item for juvenile smallmouth bass but not as abundant in the primarily piscivorous and insectivorous diets of age-1 or younger walleye. Similarly, Frey *et al.* (2003) determined that adult walleye and smallmouth bass diets were markedly different in Big Crooked Lake, Minnesota with walleye preying primarily on yellow perch while crayfish were proportionally the largest prey item for smallmouth bass.

Diet overlap between species may only occur seasonally. Raborn *et al.* (2004) determined that walleye had significant diet overlaps with black crappie and largemouth bass during spring and winter seasons but that their diets differed more throughout the summer and fall periods. In that study, diet overlap was largely attributed to a singular prey group (*Dorosoma* spp.). Age-0 and age-1 diets were compared seasonally between walleye, black crappie, largemouth and smallmouth bass and diet overlap between walleye and the other species was largely dependent on the timing of ontogenetic diet shifts to piscivory in walleye (Pellham *et al.* 2001). In their study, the greatest diet overlap occurred between walleye and largemouth bass but the relationship was highly seasonal.

Rainbow smelt (*Osmerus mordax*) are an introduced species in Ontario that can also affect walleye populations. Young-of-year walleye abundance was reduced by an average of 13% in 10 Wisconsin lakes following the invasion of rainbow smelt (Mercado-Silva *et al.* 2007). In the Bay of Quinte, Lake Ontario, rainbow smelt are an important diet item for walleye but high abundance of rainbow smelt have also been suspected of limiting walleye recruitment due to the fact that smelt may also be a competitor or predator of walleye fry (Bolby *et al.* 2010). Modeling results suggest that the effect of rainbow smelt's dominance of the Sparkling Lake, Wisconsin fish community was due to multiple interactions between walleye, rainbow smelt and lake herring (*Coregonus artedi*) (Roth *et al.* 2010).

Larval and juvenile walleye are most vulnerable to predation, but in some fish communities, adult walleye may also be prey (Nate *et al.* 2011). Esocids are top predators that occur with walleye across much of the Ontario range and may prey upon larger sizes of walleye. Interestingly, Knapp *et al.* (2012) found no significant decline in walleye catch per unit effort (CUE) following the introduction of muskellunge (*Esox masquinongy*). The presence of muskellunge also had no effect on the success of stocked walleye (Nate *et al.* 2003). Fayram *et al.* (2005) found that muskellunge and walleye abundances were positively correlated in electrofishing surveys but had no relationship in creel survey data across a broader set of lakes. Conversely, the presence of northern pike (*E. lucius*) was cited as one factor that might limit the success of establishing self-sustaining walleye populations in northern Wisconsin lakes (Nate *et al.* 2003). Johnson *et al.* (1996) found that almost half of the over-winter mortality of stocked walleye was due to cannibalism and predation from northern pike. Northern pike and walleye abundance however were not found to be significantly correlated in 120 northern Wisconsin lakes (Fayram *et al.* 2005).

Sauger are found sporadically throughout Ontario lakes and are known to naturally hybridize with walleye (Scott and Crossman 1979). Resource overlap between walleye and sauger was found to be high in the Middle Missouri River, Montana suggesting that competition may exist between these two species. In Lake of the Woods, Minnesota, the importance of individual prey species was similar between walleye and sauger older than age-0, however, the two species appeared to be spatially segregated (Swenson and Smith 1976). Swenson and Smith (1976) were not able to isolate differences between intra and interspecific competition between walleye and sauger.

Taken together, the available information indicates that the potential exists for a number of species in Ontario to compete with walleye. To date, much of the research regarding predation on walleye fry has focused on the success of walleye stocking (Johnson *et al.* 1996, Nate *et al.* 2003, Hoxmeier *et al.* 2005) and may not be directly applicable to native walleye populations. With the exception of the analysis by Nate *et al.* (2003), most studies have considered only a small group of lakes and the majority have tried to quantify interactions between walleye and a species in isolation of other fish community effects. Thus, there is currently a need for a large scale analysis that considers how walleye populations are affected by interspecific relationships within a diversity of fish communities. The objective of this study is to examine whether there is evidence of centrarchid competition with walleye across a diversity of habitats, fish communities and fishing pressure. I will use an existing habitat model to account for differences in walleye abundance across a diversity of habitats and propose a simplified Schaeffer model to account for community and fishing effects. I hypothesize that i) walleye abundance is influenced by community effects, ii) walleye abundance will be lower in lakes where competitors are present and iii) walleye abundance will be negatively correlated with abundance of competitor species.

Chapter 3

Methods

3.1 Competition Model Development

Walleye and fish community data were broadly collected through the Ontario Fall Walleye Index Netting (FWIN) (Morgan 2002) program. This assessment data spanned a broad geographical range that captures a large spectrum of fish communities and fisheries. It is necessary to account for differences in fishing effort and habitat between lakes prior to assessing the effect of community on walleye abundance. I adapted the well-known logistic model to demonstrate how fish community and habitat interact to determine carrying capacity. I then extended the model to a Schaefer model (Schaefer 1954) to include the effects of fishing on the fish abundance. The extended model is then used to test the hypothesis that fish community has an effect of walleye abundance.

An unfished population is expected to reach an equilibrium state often referred to as the carrying capacity (k). If the fished population follows a Schaefer model of population growth, it is expected that the abundance will fluctuate around an equilibrium biomass (B_E) determined by the unfished maximum population size (k), the intrinsic rate of growth (r) and the fishing rate (F):

$$B_E = k\left(1 - \frac{F_E}{r}\right) \tag{1}$$

As fishing increases, the population will decline, eventually to a point of extinction. The rate of fishing that causes extinction is defined as F_{ext} (Figure 1).

It is hypothesized that carrying capacity is a product of both physical habitat (k_{hab}) and fish community (k_{comm})

$$k = k_{hab} \cdot k_{comm} \tag{2}$$

It is expected that a competitive fish community would decrease the carrying capacity and fished population (Figure 1). The intrinsic rate of increase (r) is a variable also required in the Schaefer model to determine B_E. Hunt *et al.* (2011, Appendix 1) provide the rational that the intrinsic rate of growth can be expressed as a function of natural mortality (M)

$$r = 2 \cdot M \tag{3}$$

A Taylor Series expansion of e^{-x}, where x<1, approximates to 1-x. Thus, if F/r is small, it can be approximated as $e^{-F/r}$.It is expected that F_{ext}=2M and thus it is expected that F_E/2M will be less than one. Therefore the model can be approximated as:

$$B_E = k \cdot e^{-\frac{F}{r}} \tag{4}$$

Also, in the recreational walleye fishery, the harvest rate is a function of angler effort and catchability,

$$F_E = q_{angling} \cdot E \tag{5}$$

Natural mortality (M) has been shown to be a function of climate (Colby and Nepszy 1981) with a recent review (Bozek *et al.* 2011b) proposing that for walleye

$$M = 0.13 \left(\frac{GDD}{1000} \right) \tag{6}$$

Substituting equations 5 and 6 in equation 1 and defining G=GDD/1000 yields:

$$B_E = k \cdot e^{-\beta \cdot \left(\frac{E}{G} \right)} \tag{7}$$

Where:

$$\beta = \frac{q_{angling}}{2 \cdot (0.13)} \tag{8}$$

When equation 2 replaces k, B_E is described as a function of habitat, fish community and fishing effort:

$$B_E = k_{hab} \cdot k_{comm} \cdot e^{-\beta \cdot \left(\frac{E}{G}\right)} \tag{9}$$

Competitive models have been proposed in many ecological and fisheries contexts but are typically based on an assumption of an understanding of the interaction. For instance, predator-prey relationships are often represented using modernized versions of the classic Lotka-Volterra model (Krebs 1994). As an exploratory model to represent a range of possible competitive processes, I propose that the community effect be represented as an exponential function where C is a descriptor of the fish community and α is the overall effect of fish community (C).

$$k_{comm} = e^{\alpha C} \tag{10}$$

Community effects may have positive effects, such as highly valued prey items or negative effects (e.g. high competitor or predator abundance). With a diversity of species present, fish community (C) can also be the sum of several species effects:

$$\alpha C = \sum_{i=n}^{n} \alpha_1 C_1 + \ldots + \alpha_n C_n \tag{11}$$

FWIN surveys provide a measure of relative abundance as CUEW (CUE expressed as kg/net) which is related to B_E through the FWIN catchability such that:

$$CUEW = q_{FWIN} \cdot B_E \tag{12}$$

When equations 10 and 12 are substituted in equation 9 and isolated for CUEW the model is:

$$CUEW = q_{FWIN} \cdot k_{hab} \cdot e^{\alpha C} \cdot e^{-\beta\left(\frac{E}{G}\right)} \tag{13}$$

Hunt *et al.* (2011) show that for a logistic model, k for walleye can be calculated if the maximum sustained yield (MSY) is known:

$$k = \frac{4\,MSY}{r} = \frac{4 \cdot MSY}{2 \cdot 0.13 \cdot G} \qquad (14)$$

Lester *et al.* (2004) determined that habitat and climate were important factors in determining walleye maximum sustained yields (MSY) in Ontario lakes however fish community was not considered in the model. Thus estimates of MSY from Lester *et al.* (2004) can be used to determine k_{hab}. Appendix A summarizes the method from Lester *et al.* (2004) for calculating MSY for walleye in Ontario from the thermal optical habitat area index (TOHAI) and total dissolved solids (TDS) such that:

$$MSY = 0.011 \cdot TOHAI \cdot TDS^{0.534} \qquad (15)$$

Equation 13 can be $\log_e$ transformed to make an additive model that can be used to estimate α and β through multiple regression. I assume that in the absence of fishing effort and community effect walleye abundance will reach k_{hab} and thus to test for fishing and community effects I considered the following model:

$$\log_e\left(\frac{CUEW}{k_{hab}}\right) = \alpha C - \beta\left(\frac{E}{G}\right) + \log_e\left(q_{FWIN}\right) \qquad (16)$$

3.2 Walleye Abundance

Between 1993 and 2003, 479 FWIN projects were conducted on 401 different waterbodies distributed widely throughout Ontario. The target temperature range for FWIN surveys is 10-15°C however several surveys were conducted outside the target temperature window (3.5-20.1°C). Temperature affects the metabolism and mobility of fish and has been shown to affect gill net catchability of species (Linlokken and Haugen 2006). Temperature was found to have a significant effect on walleye CUEW within the survey (Anova, p=0.02) and thus only surveys that were conducted within the target temperature range were included.

Provincial stocking records from 1974-2000 indicated that 86 lakes had been stocked with walleye. Stocking activities varied in stocking date, objective (e.g. introduction, rehabilitation) and lifestage (e.g. fry, adults). All lakes that had been stocked with walleye were excluded from the analysis. No distinction was made between lakes that had native or introduced centrarchid populations since historical stocking records may not fully document all stocking activities (e.g. illegal stocking, range extensions) and it was assumed that walleye populations at the time of sampling had already reached an equilibrium biomass.

Lakes lacking the required bathymetry data to convert catches to area weighted catches or parameters in order to estimate MSY were also excluded. In all there were 140 lakes available that were appropriate for the community analysis (Figure 2). Where lakes were sampled in more than one year, the average CUEW between all surveys is reported.

FWIN is a depth- stratified, random sampling design that uses a mixed mesh gillnet (8 meshes ranging from 25-152 mm stretch mesh). Depth stratification occurs between two strata with target depths of 2-5m and 5-15m, however some projects conducted sets outside of the target strata. Net sets are recorded with a minimum and maximum set depth with the median depth being used to assign each net to a depth stratum (<2m, 2-5m, 5-15m, >15m).

Life history characteristics of walleye were summarized for the 479 projects by Morgan *et al.* (2003) however catch was summarized as number of walleye per net for each lake. Using a biomass index (CUEW) limits the influence of large numbers of small (young) fish that may not be fully recruited to the fishery and still have high natural mortality. Biomass is also the standard measure in surplus production models and is the unit of measure in the model used to estimate MSY for walleye (Lester *et al.* 2004). Field collection of round weights were highly variable and in many cases unreliable. Weights were also not consistently collected for all species of interest.

Fork lengths (FLEN) were collected more consistently and were used to estimate round weight (RWT) using the following formula:

$$l = a\ w^{b} \qquad (17)$$

Where, l is length, w is weight and a and b are species dependent coefficients (Table 2) calculated from the examination of approximately 1 million fish (Addison pers. comm.).

Since FWIN targets only the 2-15m portion of the lake it is necessary to estimate whole lake CUEW based on the area available in the unsampled portion of the lake. Where non-target strata (< 2 or >15m) CUEWs were available, the catches from each strata were compared. There were 40 projects that had nets set in depths < 2m and in the 2-5m stratum. There were also 34 projects where sets exceed 15m and had 5-15m samples for comparison. Walleye abundance ($\log_e$(CUEW+1)) was compared between the catches in the < 2m strata to the 2-5m strata and between the 5-15m strata to the >15m strata to determine whether the prescribed strata catches (2-5m and 5-15m) could be used to estimate catches from the unsampled parts of the lake. Using the 2-5m CUEW to estimate the < 2m strata CUEW is justifiable since the 2-5m strata and the < 2m strata were highly correlated (R=0.50). The 5-15m strata CUEW was also significantly correlated with >15m depth strata CUEW (R=0.49). The majority of the surveys only sampled depths < 20m (Figure 3) and may not be representative of catches beyond those depths. Additionally, estimated thermocline depths suggest that little walleye habitat exists deeper than 15m. Only 12 of the study lakes had a thermocline greater than 15m with the greatest being 18.9m. It is assumed, for the species where CUEW was estimated, that only depth less than 15m contribute to the overall CUEW such that the whole lake CUEW was estimated as:

$$\mathrm{CUEW}_{(\mathrm{wholelake})} = \mathrm{CUEW}_{(2\text{-}5\mathrm{m})} \times \%\ \mathrm{Area}_{(<2\mathrm{m})} + \mathrm{CUEW}_{(2\text{-}5\mathrm{m})}$$
$$\times \%\ \mathrm{Area}_{(2\text{-}5\mathrm{m})} + \mathrm{CUEW}_{(5\text{-}15\mathrm{m})} \times \%\ \mathrm{Area}_{(5\text{-}15\mathrm{m})} \qquad (18)$$

Additionally, CUEW was estimated with the same methodology for seven other species (northern pike, yellow perch, lake herring, lake whitefish, smallmouth bass, white suckers and rock bass) that had length data regularly collected across all surveys.

3.3 Physical Lake Data

The analysis of walleye abundance required physical lake data to account for lake differences in habitat suitability for walleye. Application of an existing habitat model (Lester *et al.* 2004) required the following lake measurements: maximum depth, mean depth, Secchi depth, lake area, and total dissolved solids (TDS). These data were available through the Aquatic Habitat Index (AHI) surveys which were conducted between 1966 and 1986. In addition, data from some lakes were available from more recent surveys (OMNR Broadscale Monitoring Program (BSM) (Sandstrom *et al.* 2011) and the Ontario Ministry of the Environment Lake Partner Program (LPP) (OMOE 2011)). Because Secchi depth may have changed (e.g. due to the invasion of zebra mussels throughout Southern Ontario), I used more recent surveys (when available) to update Secchi depth. All other physical data were extracted from the AHI database (Appendix A).

3.4 Fish Community Sampling

FWIN gill net gangs have a minimum mesh size of 25mm stretch mesh and are not suitable to provide a full community index due to low catchability or non-vulnerability of small fish. Fish community data was obtained from the AHI surveys (Dodge *et al.* 1984) which includes gillnets with smaller mesh sizes. Due to differing methodology and gear, quantitative abundance between the two survey gears is not likely to be directly comparable without significant calibration (Jackson and Harvey 1997). Catch data from the AHI was used only to assess presence or absence of a species within the lake. Additionally, any species recorded in the FWIN survey, but not in the AHI, were included since new species may have been introduced or invaded between surveys. Community classification based on presence and absence data should still provide accurate assessments of patterns as Heino *et al.* (2010) found no significant differences in community structure when they compared presence/absence data to relative abundance as biomass. A total of 67 species were identified across the survey lakes although 10 species were omitted from the analysis as they were rare (N=1), possibly misidentified or non-reproducing stocked species (e.g. splake) (Table 3).

3.5 Effect of Angling

Over the diversity of lakes available in the FWIN surveys, individual lake assessments of fishing pressure are not available. The best available data to quantify fishing effort at this scale is available only at the Fisheries Management Zone (FMZ) (Figure 2) level derived from a mail in survey (DFO 2007). The mail survey gathers information from a random sample of anglers on the amount of time spent fishing and on which specific bodies of water. The data are extrapolated to provide estimates of fishing effort (E, hr/ha per year) at the zone level which Hogg *et al.* (2010) suggest is highly correlated with creel surveys. Angling catchability, the parameter that relates angling effort to fishing mortality ($q_{angling}$), may vary between lakes and through time but is a difficult parameter to estimate (Lester *et al.* 2003). This model includes harvest rate in the estimation of angling effect (β) (Equation 8).

3.6 Fish Community Analysis

An analysis of similarities (Clarke 1993) using a Jaccard Index of dissimilarity was conducted in R (R Development Core Team 2010) using ANOSIM in the VEGAN package (Oksanen *et al.* 2011) to determine the variability in fish communities between zones to determine whether fish communities could be assigned a categorical variable related to FMZ. The Jaccard Index is less sensitive to false absences and is the recommended index for comparing assemblages based on species presence (Kwak and Peterson 2007). Fish community similarity differed between zones (ANOSIM, P=0.001) however considerable variability existed within some zones. Fish community was most homogenous in zones 2, 4 and 17 and had the greatest diversity in 5, 8, 10 (Figure 4). The overall diversity of communities within zone was considered too diverse to assign a categorical community variable.

The Jaccard Index is a metric index and can be used as a distance measure in ordination (Magurran 2004). Multidimensional scaling (MDS) based on Jaccard dissimilarities was conducted to assign a continuous scale of community classification. MDS is more robust than other ordination techniques in the face of irregular distributions and high sampling variance and has become a preferred technique in fish community ordination (Rice 2000). MDS was conducted in R (R Development Core Team 2010) using metaMDS in the VEGAN package (Oksanen *et al.* 2011). I used 100 random starts in metaMDS in order to find a global solution as MDS can be easily trapped at a local optima (Oksanen *et al.* 2011) where a new solution with a lower stress value is retained as the ‘best solution’. Where stress values are close, metaMDS conducts a Procrustes Analysis to find a convergent solution. In order to achieve a stress coefficient below the recommended threshold of 15% (Kruskal and Wish 1984), four dimensions were required (Figure 5). A convergent solution was found in five attempts and had a stress value of 12.96%.

3.7 Model Analysis

Community effects were first considered using the results from the MDS. The axes of a MDS can be used as orthogonal predictors in a multiple regression (Quinn and Keogh, 2002). The first multiple regression model (model = ORD) tested defined fish community (C) as the MDS scores on each axis.

$$\alpha C = \alpha_1 \mathit{Axis1} + \alpha_2 \mathit{Axis2} + \alpha_3 \mathit{Axis3} + \alpha_4 \mathit{Axis4} \tag{19}$$

The full model is:

$$\begin{aligned} \log_\mathrm{e}\left(\frac{CUEW}{k_{hab}}\right) &= \alpha_1 \mathit{Axis1} + \alpha_2 \mathit{Axis2} + \alpha_3 \mathit{Axis3} + \alpha_4 \mathit{Axis4} \\ &\quad - \beta\left(\frac{E}{G}\right) + \log_e\left(q_{FWIN}\right) \end{aligned} \tag{20}$$

Significant axes were then examined using species scores to determine whether effects of individual species presence could yield a better model than MDS scores. Centrarchid species (model=CENT), species of interest for management (MGT) as well as species with strong MDS effect on Axes 2 and 4 (model=FULL) were examined. Quinn and Keogh (2002) suggest that the number of predictors be limited by the sample size where the sample size should remain greater than 6-10 times the number of predictors. For a sample size of 140 lakes, I choose the conservative ratio of 10:1 (sample size: predictors) limiting predictors to a maximum of 14. Fishing effort (E/G) was included as a predictor in all models and thus a maximum of 13 species could be included in model FULL.

Table 4 summarizes the presence/absence models considered. Catch per unit effort (CUEW, kg/net) was calculated for seven species commonly caught throughout the FWIN surveys. In order to test the hypothesis that walleye abundance is negatively correlated to competitor abundance each species CUEW along with fishing effort was considered as an additional model where αC was:

$$\begin{aligned}\alpha C = {} & \alpha_1 CUEW_{SmBas} + \alpha_2 CUEW_{NoPik} + \alpha_3 CUEW_{RoBas} \\ & + \alpha_4 CUEW_{LaHer} + \alpha_5 CUEW_{LaWhi} + \alpha_6 CUEW_{YePer} \\ & + \alpha_7 CUEW_{WhSuc}\end{aligned} \tag{21}$$

The assumptions of a linear model were tested using the GVLMA test (Pena and Slate, 2010). Model selection was conducted using an all models approach using the dredge function in the MuMIn library (Barton, 2011) in R (R Development Core Team, 2010). Akaike information criteria for small sample sizes (AIC_c) was used to rank models. AIC_c is recommended when the ratio of sample size to predictors is less than 40 (Burnham and Anderson, 2002). Models with a difference of less than three AICc are considered to be as good as the best approximating model (Burnham and Anderson, 2002). Model reduction, based on the principles of parsimony (Crawley, 2007), was then conducted in order to find a model that was minimal adequate. Nested models were compared using an Anova. When a nested model was not significantly different ($p<0.05$) than the full model, the nested model was deemed the better model.

Fry predation is one hypothesis that has been suggested as a means of competition between walleye and centrarchid species. It is hypothesized that if walleye fry predation was an underlying competitive mechanism, a species with similar vulnerabilities may show similar abundance patterns. White suckers are a species that has similar thermal preference and spawning habitats as walleye but is not exploited to the same degree in the recreational fishery

(Scott and Crossman, 1979). An exploratory analysis was conducted to compared walleye abundance and habitat (k_{hab}) to white sucker abundance using a linear regression.

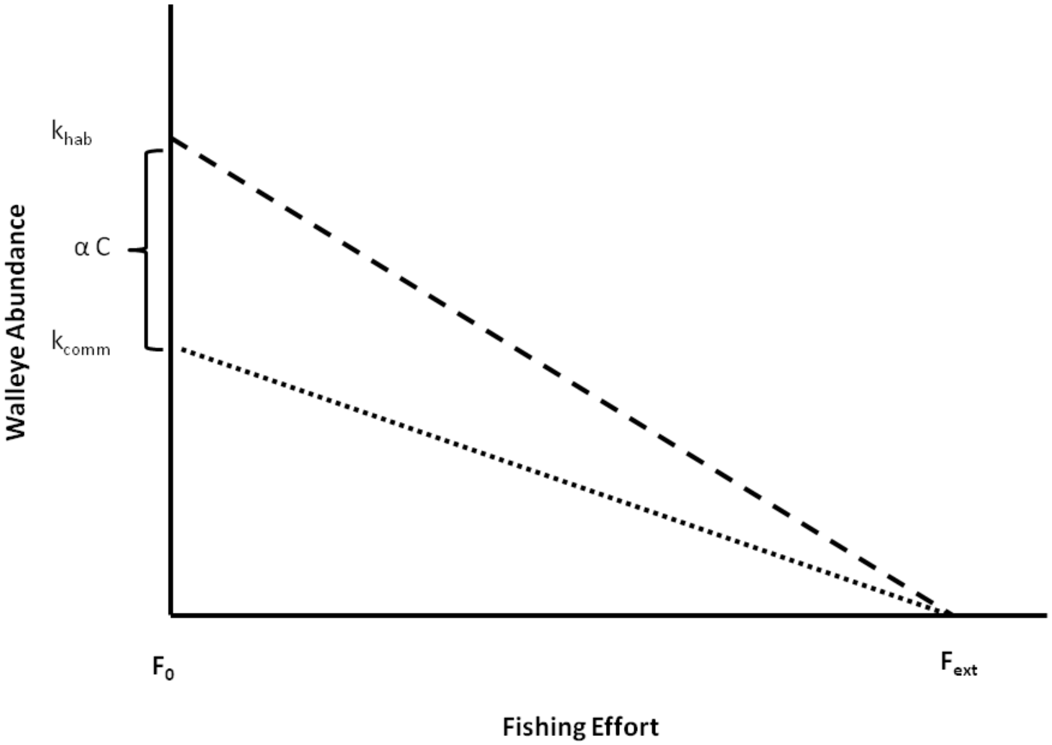

Figure 1. Hypothetical model used to test for community effects on walleye abundance across a gradient of habitat and fishing conditions. Habitat availability will determine a carrying capacity (k_{hab}) in an unfished (F_0) system. As fishing effort increases, abundance will decline (dashed line) to a point where fishing effort causes extinction (F_{ext}). A competitive fish community (αC) will reduce the unfished carrying capacity (k_{comm}) and abundance across all levels of fishing effort (dotted line).

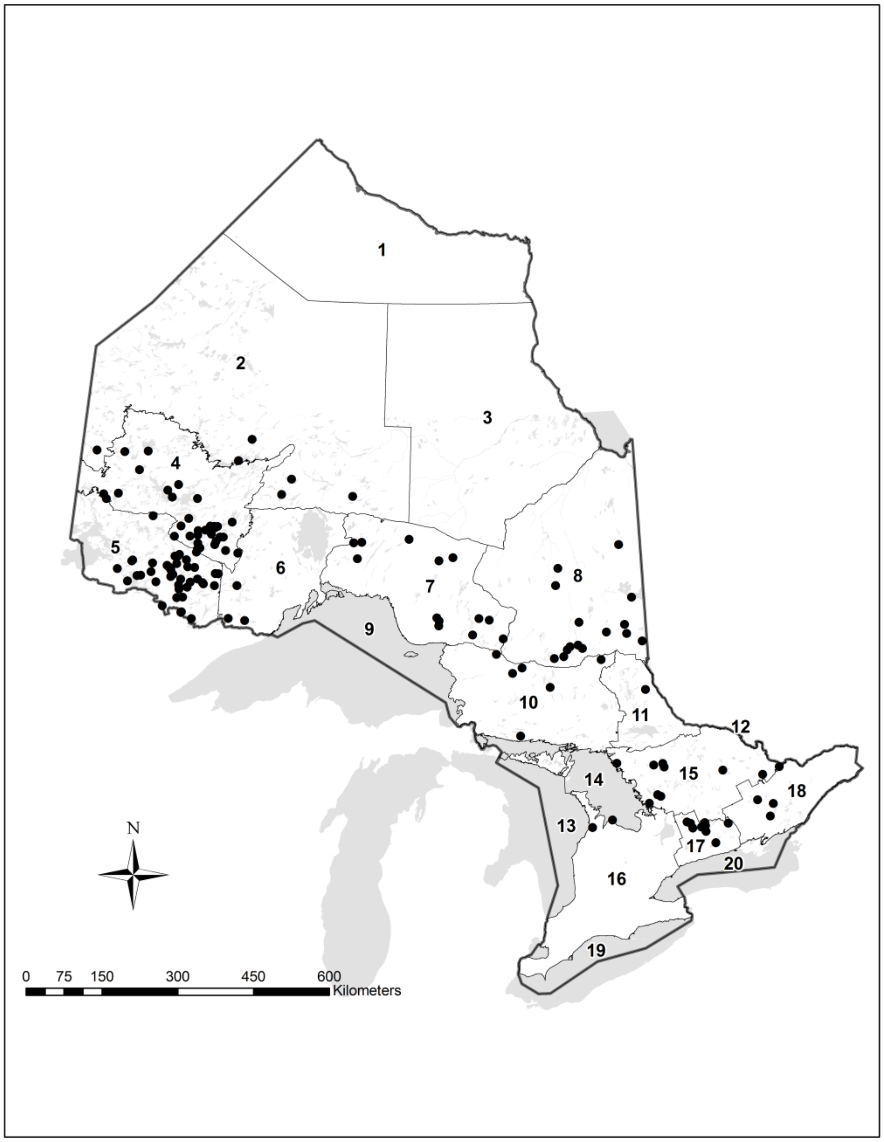

Figure 2. Lakes surveyed (dots) with the Fall Walleye Index Netting Protocol (FWIN) spanned across a large proportion of Ontario and within the majority of Fisheries Management Zones (FMZ) (indicated by number). Estimates of fishing effort were derived from a mail in survey and are reported at the FMZ level.

Table 2. Conversion values used to determine round weight (w) (RWT, grams) from fork length (l) (FLEN, mm) where $l = a\,w^b$ for eight species regularly captured and measured during the Fall Walleye Index Netting (FWIN) surveys.

Species	a	b
Lake herring	2.98×10^{-6}	3.27
Lake whitefish	6.26×10^{-6}	3.12
Northern pike	2.66×10^{-6}	3.16
Rock bass	1.26×10^{-5}	3.11
Smallmouth bass	5.17×10^{-6}	3.21
Walleye	5.12×10^{-6}	3.13
White sucker	1.14×10^{-5}	3.04
Yellow perch	5.78×10^{-6}	3.17

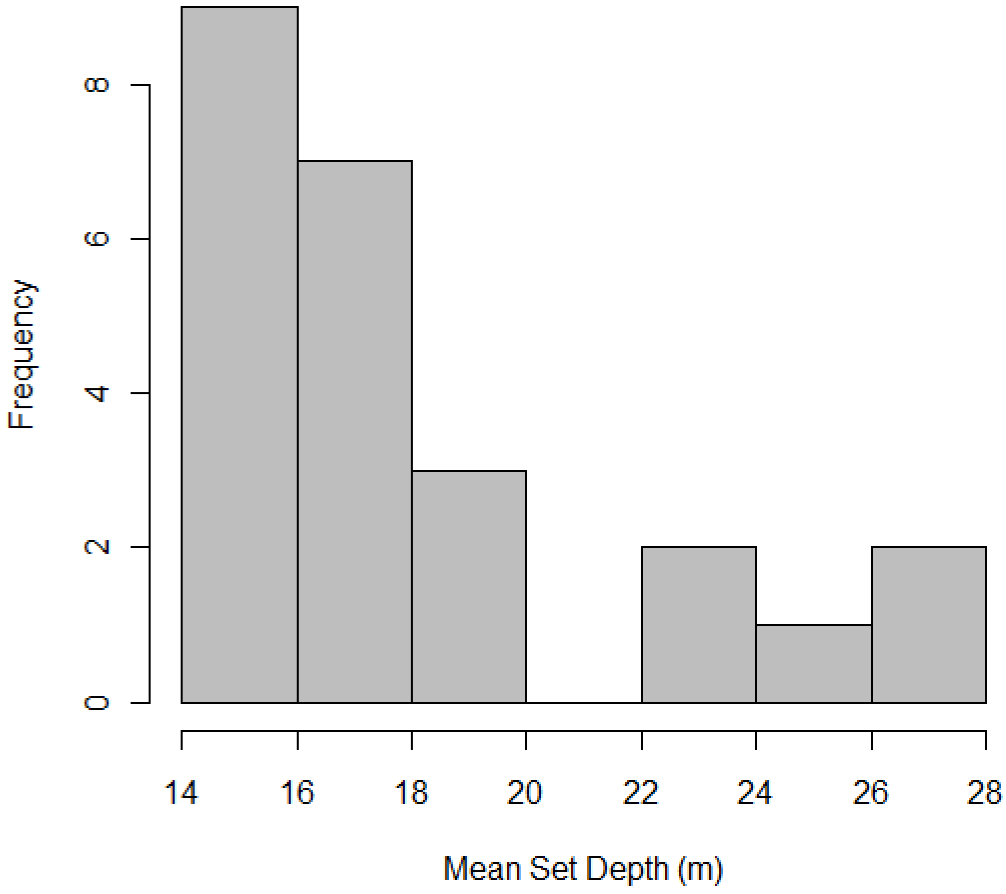

Figure 3. Distribution of mean depth (m) of net sets in depths greater than 15m across 140 Ontario lakes surveyed with the Fall Walleye Index Netting (FWIN) protocol.

Table 3. Species caught in 140 Fall Walleye Index Netting (FWIN) surveys in Ontario between 1993-2003. Asterisk (*) indicates species that were omitted from the fish community analysis.

Common Name	Scientific Name	Label	Lakes
Banded Killifish	*Fundulus diaphanus*	BaKil	5
Black Crappie	*Pomoxis nigromaculatus*	BlCra	7
Blackchin Shiner	*Notropis heterodon*	BcShi	7
Blacknose Dace	*Rhinichthys atratulus*	BnDac	4
Blacknose Shiner	*Notropis heterolepis*	BnShi	45
Bluegill	*Lepomis macrochirus*	Blueg	10
Bluntnose Minnow	*Pimephales notatus*	BnMin	42
Bowfin*	*Amia calva*	Bowfi	1
Brassy Minnow	*Hybognathus hankinsoni*	BrMin	2
Brook Stickleback	*Culaea inconstans*	BrSti	15
Brook Trout	*Salvelinus fontinalis*	BkTro	3
Brown Bullhead	*Ameiurus nebulosus*	BrBul	22
Burbot	*Lota lota*	Burbo	77
Central Mudminnow	*Umbra limi*	CeMud	7
Channel Catfish*	*Ictalurus punctatus*	ChCat	1
Common Carp	*Cyprinus carpio*	CoCar	7
Common Shiner	*Luxilus cornutus*	CoShi	16
Creek Chub	*Semotilus atromaculatus*	CrChu	8
Deepwater Sculpin*	*Myoxocephalus thompsoni*	DwScu	1
Emerald Shiner	*Notropis atherinoides*	EmShi	17
Fallfish	*Semotilus corporalis*	Fallf	4
Fathead Minnow	*Pimephales promelas*	FhMin	16
Finescale Dace	*Phoxinus neogaeus*	FsDac	7
Freshwater Drum*	*Aplodinotus grunniens*	FwDru	1
Golden Shiner	*Notemigonus crysoleucas*	GoShi	29
Goldeye*	*Hiodon alosoides*	Golde	1
Iowa Darter	*Etheostoma exile*	IoDar	59
Johnny Darter	*Etheostoma nigrum*	JoDar	52
Lake Chub	*Couesius plumbeus*	LaChu	9
Lake Herring	*Coregonus artedi*	LaHer	107
Lake Sturgeon	*Acipenser fulvescens*	LaStu	7
Lake Trout	*Salvelinus namaycush*	LaTro	28

Lake Whitefish	*Coregonus clupeaformis*	LaWhi	102
Largemouth Bass	*Micropterus salmoides*	LmBas	18
Logperch	*Percina caprodes*	Logpe	45
Longear Sunfish	*Lepomis megalotis*	LeSun	4
Longjaw Cisco*	*Coregonus alpenae*	LjCis	1
Longnose Dace	*Rhinichthys cataractae*	LnDac	22
Longnose Sucker	*Catostomus catostomus*	LnSuc	12
Mimic Shiner	*Notropis volucellus*	MiShi	39
Mooneye	*Hiodon tergisus*	Moone	7
Mottled Sculpin	*Cottus bairdi*	MoScu	33
Muskellunge	*Esox masquinongy*	Muske	16
Ninespine Stickleback	*Pungitius pungitius*	NiSti	14
Northern Hog Sucker*	*Hypentelium nigricans*	NHSuc	1
Northern Pike	*Esox lucius*	NoPik	129
Northern Redbelly Dace	*Phoxinus eos*	NRDac	12
Pearl Dace	*Margariscus margarita*	PeDac	8
Pumpkinseed	*Lepomis gibbosus*	Pumpk	32
Quillback*	*Carpiodes cyprinus*	Quill	1
Rainbow Smelt	*Osmerus mordax*	RaSme	10
Rainbow Trout*	*Oncorhynchus mykiss*	RaTro	1
River Darter	*Percina shumardi*	RiDar	3
Rock Bass	*Ambloplites rupestris*	RoBas	68
Round Whitefish	*Prosopium cylindraceum*	RoWhi	2
Sauger	*Sander canadense*	Sauge	27
Shorthead Redhorse	*Moxostoma macrolepidotum*	ShRed	51
Silver Redhorse	*Moxostoma anisurum*	SiRed	12
Slimy Sculpin	*Cottus cognatus*	SlScu	8
Smallmouth Bass	*Micropterus dolomieu*	SmBas	76
Splake*	*Salvelinus fontinalis × Salvelinus namaycush*	Splak	2
Spottail Shiner	*Notropis hudsonius*	SpShi	82
Tadpole Madtom	*Noturus gyrinus*	TaMad	7
Trout-perch	*Percopsis omiscomaycus*	TrPer	37
Walleye	*Sander vitreum*	Walle	140
White Sucker	*Catostomus commersoni*	WhSuc	139
Yellow Bullhead	*Ameiurus natalis*	YeBul	2
Yellow Perch	*Perca flavescens*	YePer	139

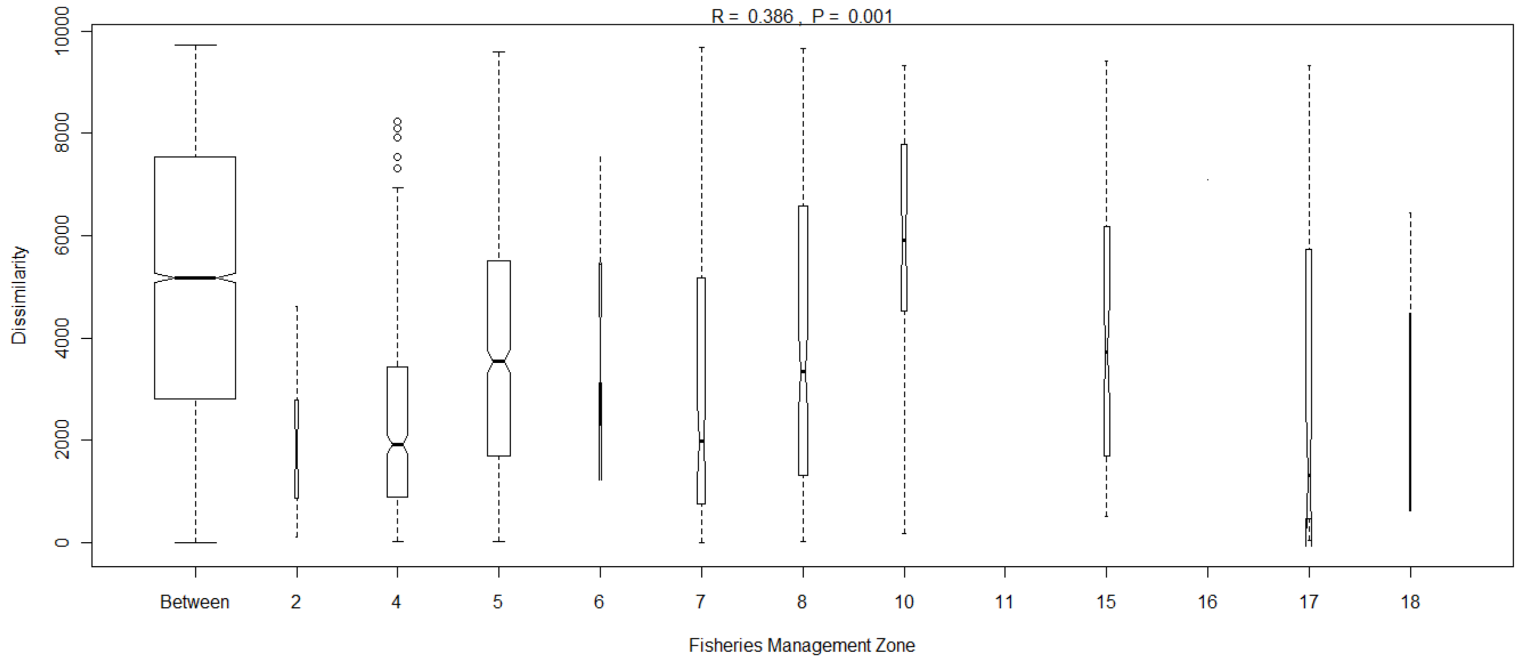

Figure 4. Analysis of similarities of fish community diversity across Fisheries Management Zones (FMZs). Fish community dissimilarity was calculated using the Jaccard Index of dissimilarity using the presence/absence of fish species. Fish community similarity differed between Zones (ANOSIM statistic R=0.386, P=0.001). Box widths are scaled to sample size ($\sqrt{N}$), box denotes inter quartile range (IQR) and whiskers are 1.5x IQR. There is strong evidence to conclude that group means differ when boxplot notches do not overlap (Chambers *et al.* 2003). FMZs listed without a corresponding box (FMZs 11 and 16) have sample sizes of 1 and 2, respectively. FMZs where N=0 have been omitted.

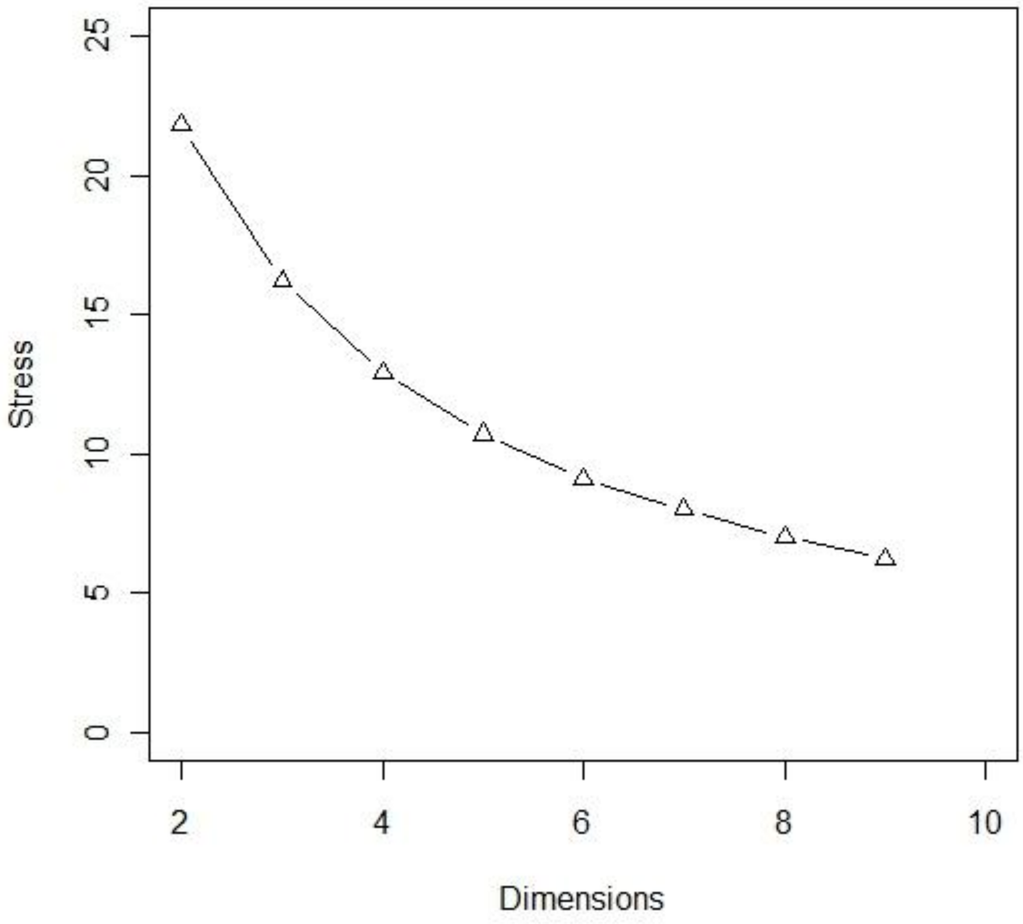

Figure 5. Stress values for multidimensional scaling using 2-9 dimensions to determine the minimum number of dimensions required for multidimensional scaling of fish community similarity based on Jaccard Index of dissimilarity. A stress value of less than 15 is recommended to provide reliable scaling results (Kruskal and Wish 1984).

Table 4. Summary of full models that consider different measures of fish community used multiple regression model search. Axis refers to the axis score derived from multidimensional scaling. Individual species abbreviations are listed in Table 3 and E/G is a measure of fishing effect.

Model Name	Full Model
ORD	$\log(CUEW/k_{hab})$= Axis1+Axis2+Axis3+Axis4+(E/G)
CENT	$\log(CUEW/ k_{hab})$=BlCra+Blueg+LeSun+LmBas+Pumpk+RoBas+SmBas+(E/G)
MGT	$\log(CUEW/ k_{hab})$=BlCra+Blueg+LaHer+LaTro+LmBas+Muske+NoPik+Sauge+SmBas+YePer+(E/G)
FULL	$\log(CUEW/ k_{hab})$=Blueg+BnShi+IoDar+JoDar+LaHer+LmBas+LnDac+Muske+NRDac+Pumpk+RoBas+Sauge+SmBas+(E/G)

Chapter 4

Results

4.1 Community Assemblage

Multidimensional scaling showed no obvious grouping of fish communities among lakes (Figure 6). Lakes in Ontario where walleye occur have a diversity of fish species present throughout the range. Environmental factors contributed to community assemblages. Lake area was positively correlated with Axis 1 and Axis 3 and negatively correlated with Axis 2 (Table 5). Axis 4 was the only axis that was correlated with Secchi depth. Axis 1 and 2 were both positively correlated with GDD and TDS. Warmwater species such as bluegill, largemouth bass and common carp orient positively on Axes 1 and 2 (Figure 7). Rare species such as round whitefish, longeared sunfish and rainbow smelt tended to separate along Axis 3.

4.2 Walleye Abundance and Habitat

Walleye catches ranged between 0.17 and 32.9 kg/ha with 50% of the lakes falling between 2.1 and 7.8 kg/ha (Figure 8). Habitat availability (k_{hab}) ranged between 0.6 and 20.7 kg/ha across all lakes (Figure 9). The range between 5 and 9.5 kg/ha represented 50% of the samples with a median of 7.3 kg/ha. The range of CUEW/k_{hab} was between 0.02 and 4.5 and 50% of the observations were between 0.3 and 1.6 (Figure 10).

4.3 Model Selection

The four starting models (ORD, CENT, FULL, and MGMT, Table 4) resulted in multiple combinations of variables. All models with a ΔAICc < 3 are referred to as 'top models'. Top models that have been reduced to minimal adequate are referred to as 'best models'. Model ORD had six top models with the best model having fishing effort and community Axis 4 as significant predictors (AICc = 339.22, adj $R^2 = 0.44$). Model CENT had 19 top models. Bluegill presence/absence and fishing effort were significant predictors in the best CENT model (AICc = 343.88, adj $R^2 = 0.42$). Model FULL had 107 top models and 5 best models. The 5 best models all had Iowa darters presence/absence, bluegills presence/absence and effort (E/G) as significant predictors with each of the 5 models having one additional species presence/absence: lake herring, pumpkinseed, smallmouth bass, northern redbelly dace and sauger. Top model statistics are in Table 6 and for each starting model (MDS, CENT, FULL and MGMT) all models with a change in AICc less than three are presented in Appendix C. Model MGT determined that the model that included the presence/absence of lake trout, bluegill and effort (E/G) was the best of the 28 top models.

Fishing effort (E/G) was an important parameter in model selection in all starting models. In an examination of FULLa it was determined that the partial r^2 of fishing effort was 0.13 which was the highest of all the parameters. The partial r^2 for bluegill, Iowa darter and lake herring were 0.07, 0.04 and 0.02 respectively. The importance of fishing effort however may be skewed as a result of fitting the model to include zone 17 (Figure 11). A linear regression between CUEW/k_{hab} and fishing effort (E/G) showed a significant relationship (R^2=0.38, p<0.001). When zone 17 lakes are excluded, less variability is explained (R^2=0.03, p=0.057) (Figure 11). When zone 17 lakes are removed from the analysis fishing effort is no longer a significant parameter in model selection.

When model selection was conducted with lakes from zone 17 omitted, there were 132 top models from model FULL and 60 top models from model MGMT. Bluegill presence/absence was a significant negative predictor in all 192 models with a median parameter value of -1.54 (IQR = 0.20) in FULL models and -1.55 (IQR=0.16) in MGMT models. Smallmouth bass presence/absence was a significant predictor in 84 of 132 FULL top models and 46 of 60 MGMT top models. The median parameter estimate for smallmouth bass presence/absence was -0.26 (IQR=0.06) in FULL and for MGMT top models the median was -0.28 (IQR=0.03). Species effect size differed between top models but only rock bass and largemouth bass presence/absence had coefficients that changed sign (N=13, min=-0.08, max=0.05 and N=18, min-0.09, max= 0.20 for rock bass and largemouth bass presence respectively).

The two best models from FULL to predict walleye CUEW were FULL i and FULL ii. The top models resulting from ORD and CENT had an ΔAICc > 3 than the best FULL and MGMT models suggesting that the best models from ORD and CENT did not provide as much explanatory power as the best models from FULL and MGMT. In the best models, fish community explains 19% of the variability of walleye catches (CUEW/k_{hab}) in lakes examined (with FMZ 17 lakes excluded). In the top models, Iowa darter presence (0.37 in both models) and lake herring presence (0.34 in both models) were positive predictors of walleye while bluegill presence (-1.54 in FULL i, -1.38 in FULL ii), smallmouth bass presence (-0.65 in FULL i) and pumpkinseed presence (-0.71 in FULL ii) were negative predictors. The presence of bluegill explained most of the variance followed by Iowa darter presence, and lake herring presence

(Table 7). Pumpkinseed and smallmouth bass explained the least amount of variance in the respective models.

4.4 Relative Abundance Model

Results for the model that used species CUEW as the community effect (equation 21) had less explanatory power (adj R^2=0.40) than models that considered only species presence/absence (adj R^2=0.44), however as with the presence/absence models fishing effort provided a large proportion of the explanatory power ($\alpha = -0.04$, partial $r^2 = 0.37$). When lakes from zone 17 were removed the best model only had an adjusted R^2 of 0.04 (p=0.01) where lake whitefish was the significant positive predictor. No negative species coefficients were predicted in any of the top models.

4.5 Relation with White Sucker Abundance

White sucker abundance was positively correlated (r=0.53, p<0.001) with walleye CUEW (Figure 12); however was not significantly correlated with k_{hab} (r= -0.05, p=0.56) (Figure 13). Lakes with bluegill or black crappie had consistently low abundance of both walleye and white sucker (Figure 14).

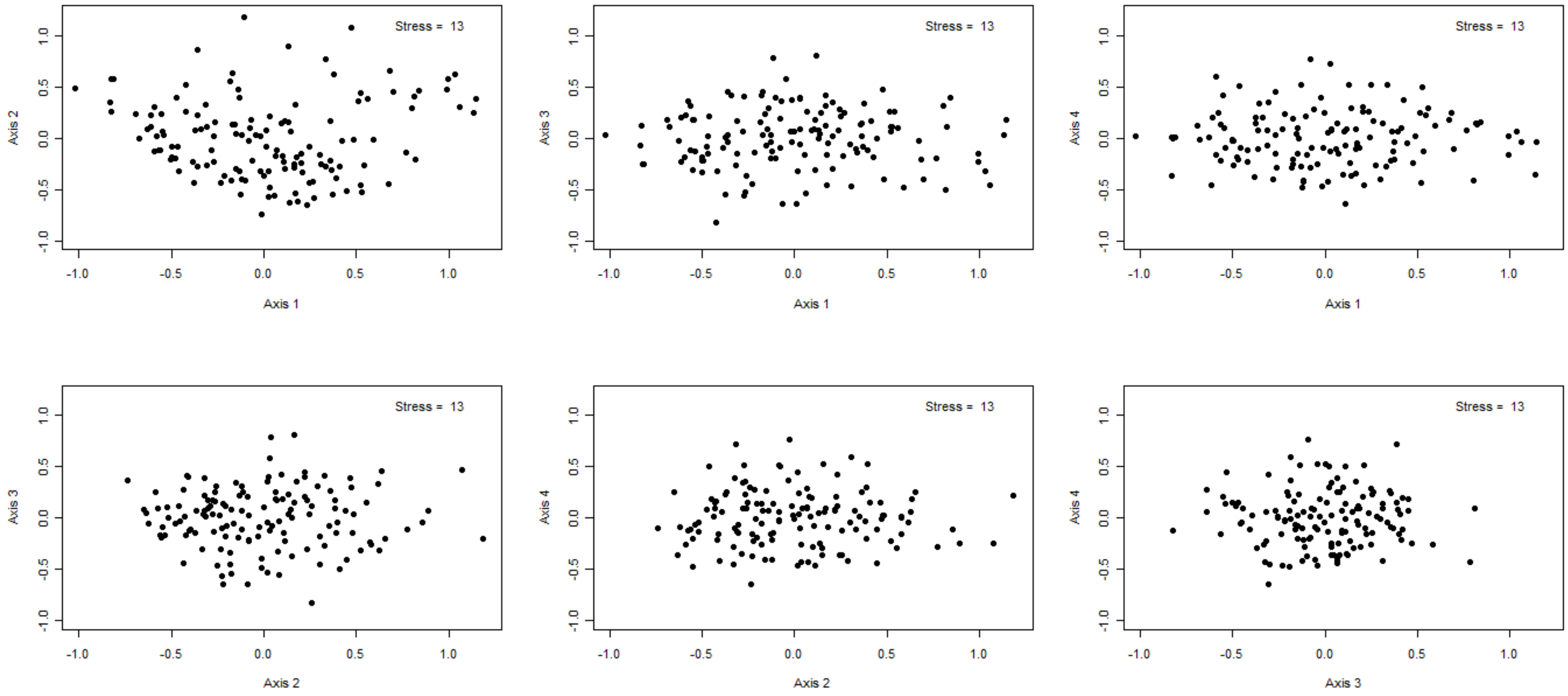

Figure 6. Multidimensional scaling (dimensions=4) of fish community similarities based on a Jaccard Index of dissimilarity using the presence/absence of 55 species in 140 lakes surveyed with Fall Walleye Index Netting and the Aquatic Habitat Survey protocols.

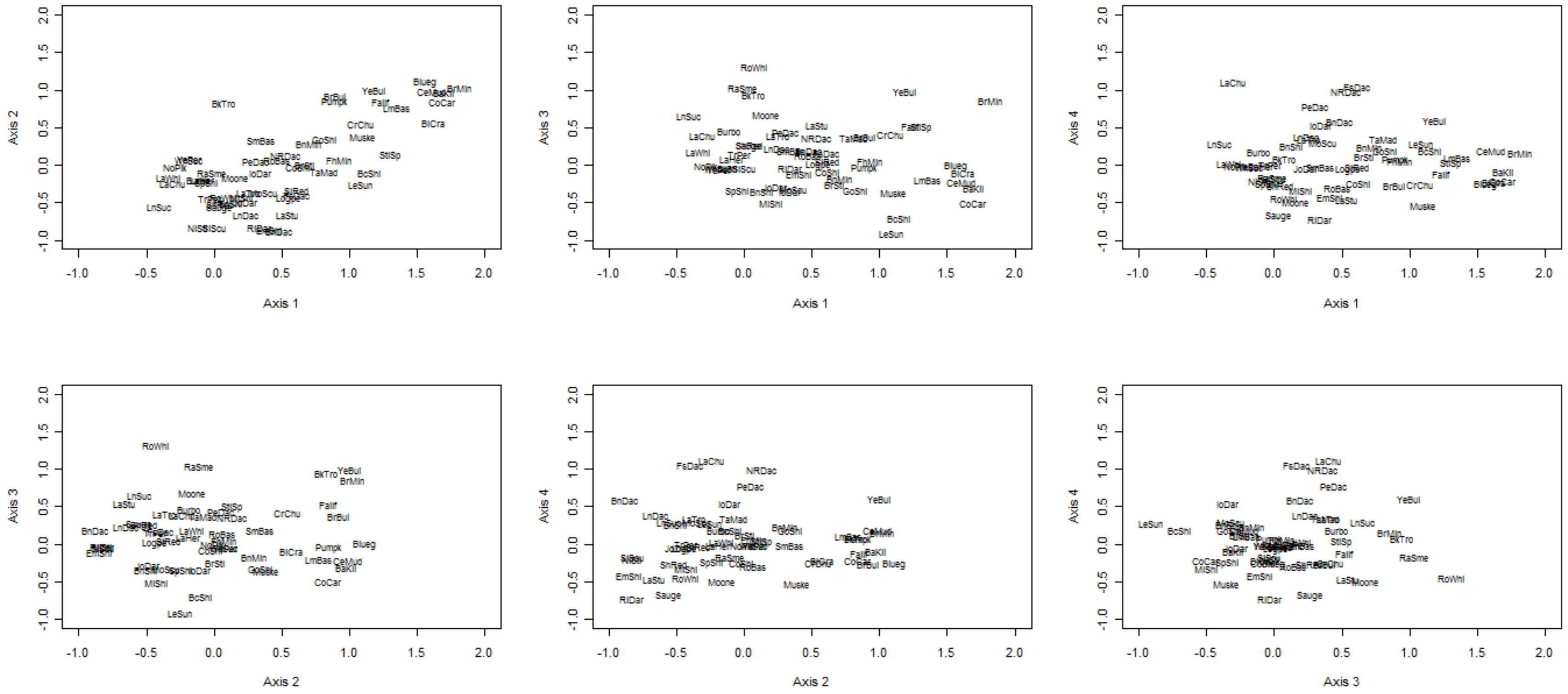

Figure 7. Species scores from multidimensional scaling (dimensions=4) of fish community similarities based on a Jaccard Index of dissimilarity using the presence/absence of 55 species in 140 lakes surveyed with Fall Walleye Index Netting and the Aquatic Habitat Survey protocols. Species abbreviations are listed in Table 3.

Table 5. Correlations between multidimensional scaling Axes and physical features (area, Secchi depth, growing degree days and total dissolved solids) of the study lakes. Bold denotes significant correlations ($p<0.5$).

MDS Axis	log(Area)	Secchi	GDD	TDS
Axis 1	**0.21 (0.02)**	0.13 (0.12)	**0.70 (<0.01)**	**0.19 (0.02)**
Axis 2	**-0.50 (<0.01)**	0.01 (0.86)	**0.46 (<0.01)**	**0.25 (<0.01)**
Axis 3	**0.29 (<0.01)**	-0.6 (0.51)	<0.01 (0.96)	-0.06 (0.44)
Axis 4	-0.08 (0.34)	**0.47 (<0.01)**	0.04 (0.65)	-0.04 (0.62)

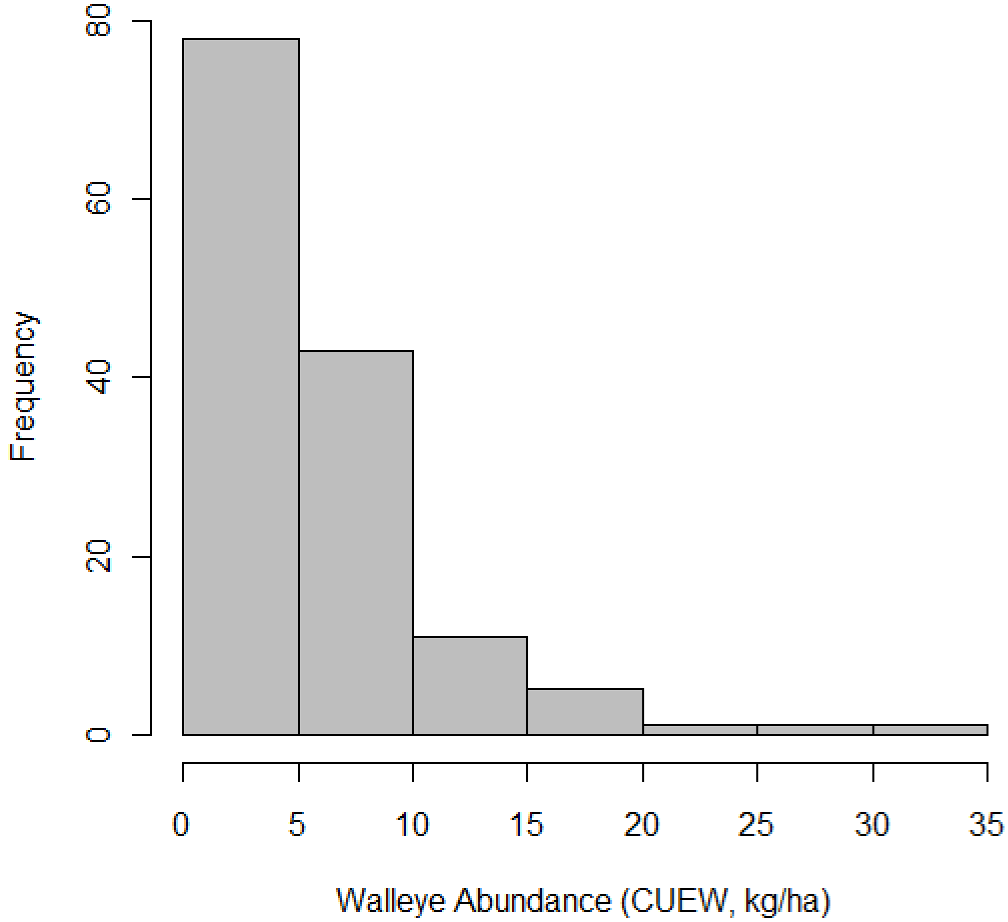

Figure 8. Frequency distribution of walleye abundance (CUEW, kg/ha) for 140 lakes surveyed with the Fall Walleye Index Netting Protocol (FWIN) in Ontario between 1993 and 2003.

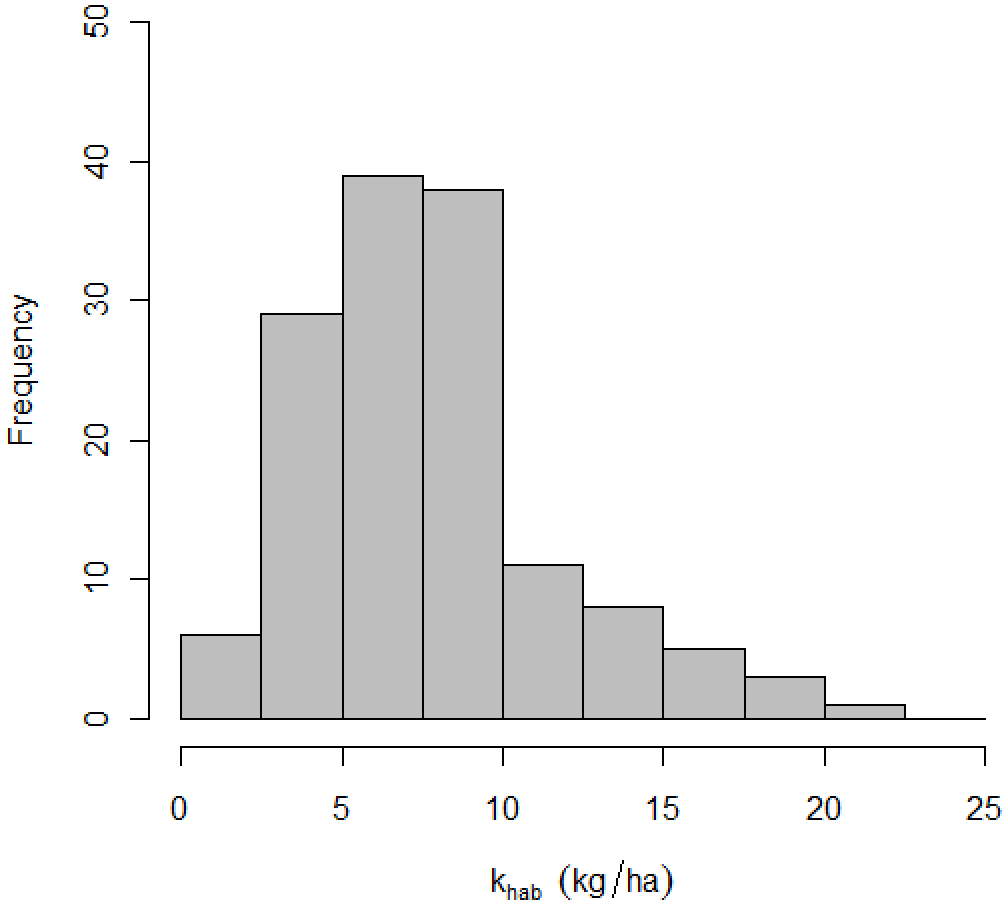

Figure 9. Frequency distribution of habitat (khab, kg/ha) for 140 lakes surveyed with the Fall Walleye Index Netting Protocol (FWIN) in Ontario between 1993 and 2003..

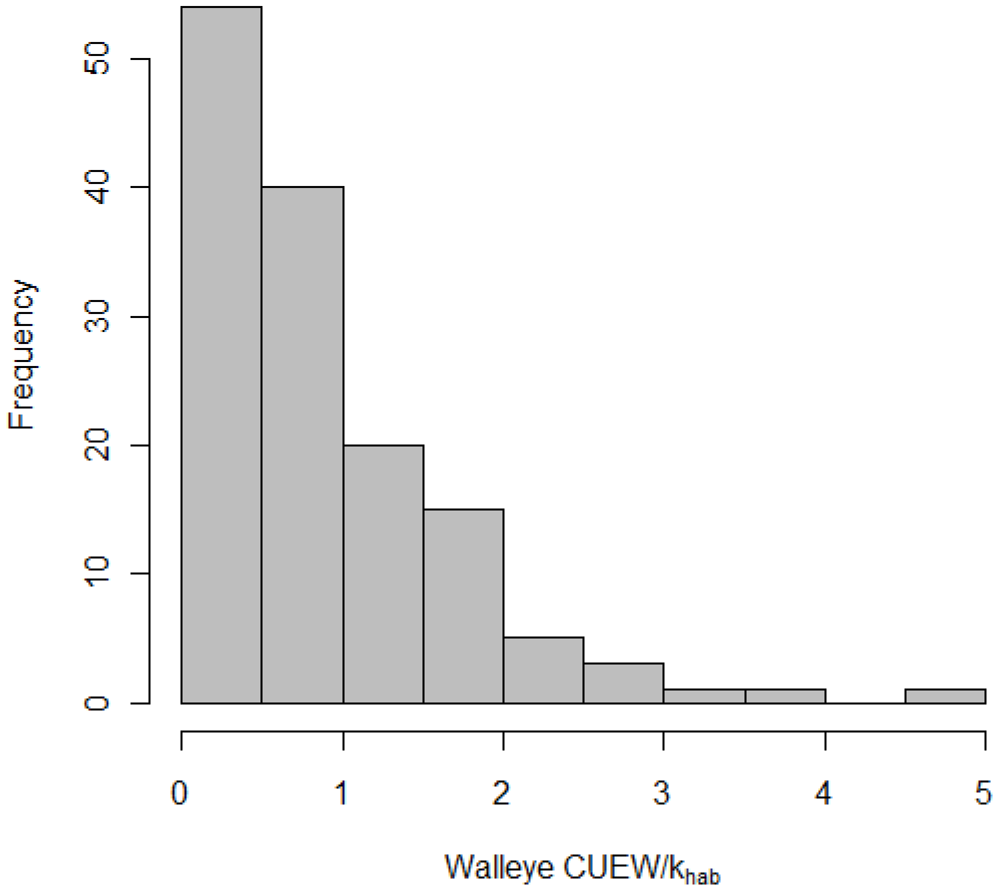

Figure 10. Frequency distribution of walleye abundance (CUEW, kg/ha) relative to available habitat (k_{hab}, kg/ha) for 140 lakes surveyed with the Fall Walleye Index Netting Protocol (FWIN) in Ontario between 1993 and 2003.

Table 6. Top model results for all lakes (a) and with FMZ 17 lakes excluded (b). Bold denotes final models.

A.

All 140 Lakes

Starting Model	Name	Candidate Model	AICc	k	adj R^2	RSE	df
FULL	FULL a	log(CUEW/k_{hab})= 0.33 (IoDar) -1.20 (Blueg) - 0.03 (E/G) + 0.27 (LaHer) - 0.52	339.19	6	0.45	0.79	135
FULL	FULL b	log(CUEW/ k_{hab})= 0.39 (IoDar) -1.08 (Blueg) - 0.03 (E/G) - 0.32 (Pumpk) - 0.30	339.21	6	0.45	0.79	135
ORD	ORD a	log(CUEW/ k_{hab})=1.02 (Axis4) - 0.04 (E/G) - 0.12	339.22	4	0.44	0.79	137
FULL	FULL c	log(CUEW/ k_{hab})= 0.39 (IoDar) - 1.16 (Blueg) -0.03 (E/G) - 0.23 (SmBas) - 0.22	339.28	6	0.45	0.79	135
FULL	FULL d	log(CUEW/ k_{hab})= 0.33 (IoDar) - 1.24 (Blueg) - 0.03 (E/G) + 0.38 (NRDac) - 0.33	339.47	6	0.45	0.79	135
MGT	MGT a	log(CUEW/ k_{hab})= 0.41 (LaTro) - 1.26 (Blueg) - 0.03 (E/G) - 0.28	340.24	5	0.44	0.8	136
FULL	FULL e	log(CUEW/ k_{hab})= 0.36 (IoDar) - 1.20 (Blueg) - 0.03 (E/G) - 0.21 (Sauge) - 0.27	340.47	6	0.45	0.79	135
CENT	CENT a	log(CUEW/ k_{hab})= -1.24 (Blueg) - 0.03 (E/G) - 0.19	343.88	4	0.42	0.81	137

B.

FMZ 17 Excluded

Starting Model	Name	Candidate Model	AICc	k	adj R^2	RSE	df
FULL	**FULL i**	**log(CUEW/ k_{hab})= 0.37 (IoDar) + 0.34 (LaHer) - 1.54 (Blueg) - 0.28 (SmBas) - 0.65**	**314.8**	**6**	**0.19**	**0.77**	**127**
FULL	**Full ii**	**log(CUEW/ k_{hab})= 0.37 (IoDar) +0.34 (LaHer) - 1.38 (Blueg) - 0.36 (Pumpk) - 0.71**	**314.8**	**6**	**0.19**	**0.77**	**127**
MGT	MGT i	log(CUEW/ k_{hab})=0.32 (LaHer) + 0.39 (LaTro) - 1.53 (Blueg) - 0.28 (SmBas) - 0.55	316.5	6	0.18	0.78	127
ORD	ORD i	log(CUEW/ k_{hab})= 0.78 (Axis4) - 0.65 (Axis2) - 0.43	322.7	4	0.13	0.81	129
CENT	CENT i	log(CUEW/ k_{hab})= -1.74 (Blueg) - 0.35	323.3	3	0.11	0.81	130

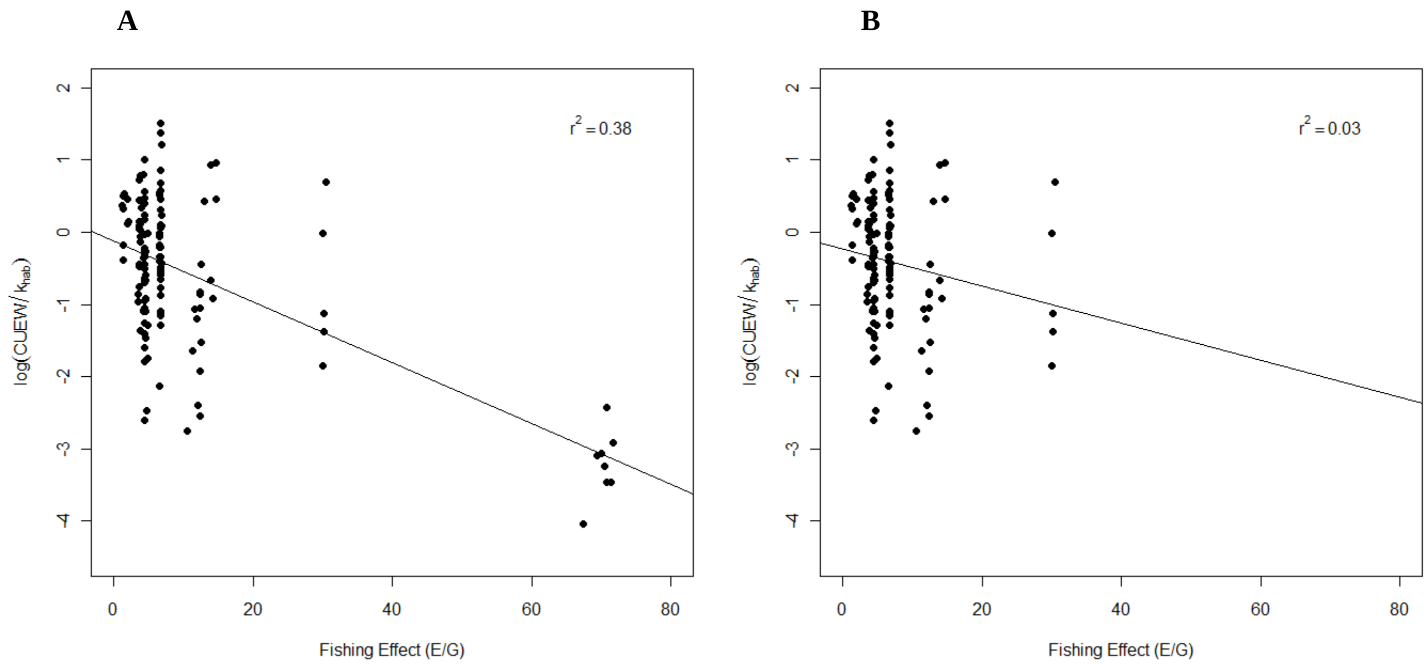

Figure 11. Linear regression of fishing effort (E/G) and walleye abundance (CUEW/k_{hab}) with zone 17 lakes included (A) (r^2=0.38, $p<0.001$) and excluded (B) (r^2=0.03, p=0.057).

Table 7. Partial r^2 explained by each species within the top two models.

Model	Blueg	IoDar	LaHer	SmBas	Pumpk
FULL i	0.1	0.05	0.04	0.03	NA
FULL ii	0.08	0.05	0.03	NA	0.03

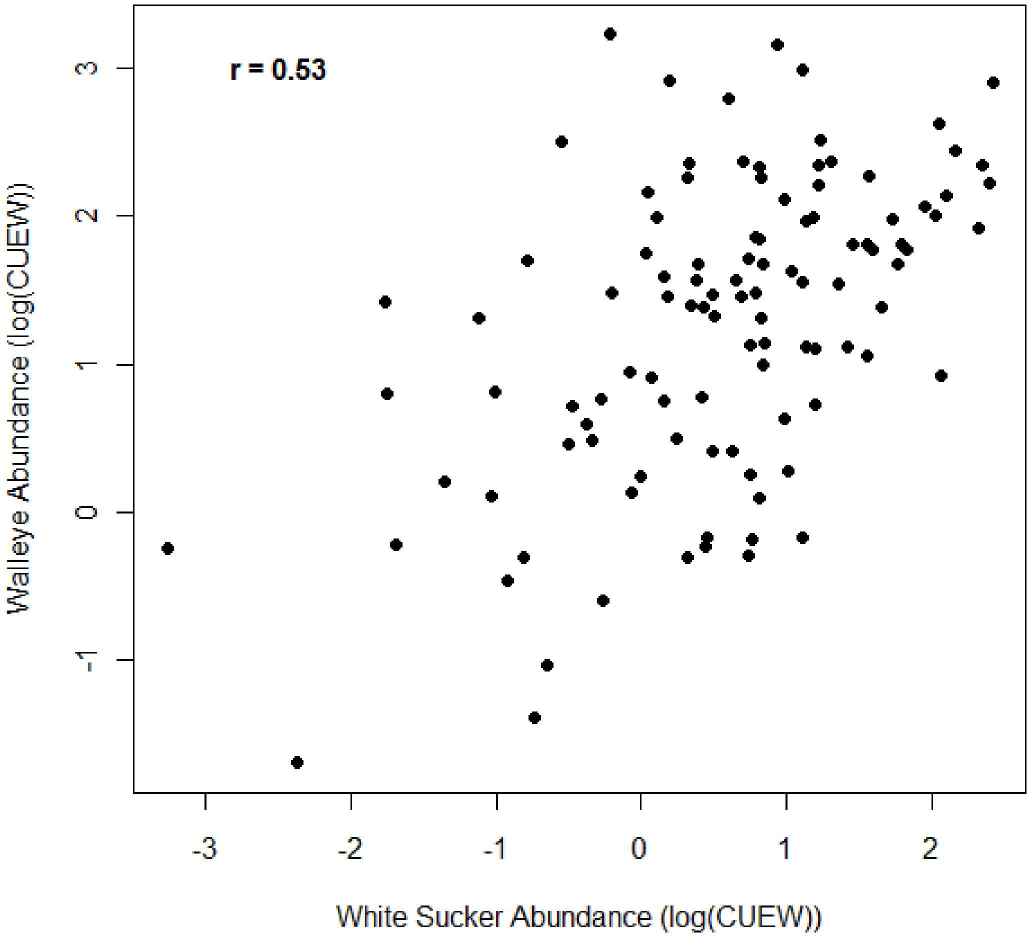

Figure 12. Correlation (p<0.001) between walleye abundance (CUEW (kg/ha)) and white sucker abundance (CUEW (kg/ha)) from 107 Ontario lakes sampled using the Fall Walleye Index Netting protocol.

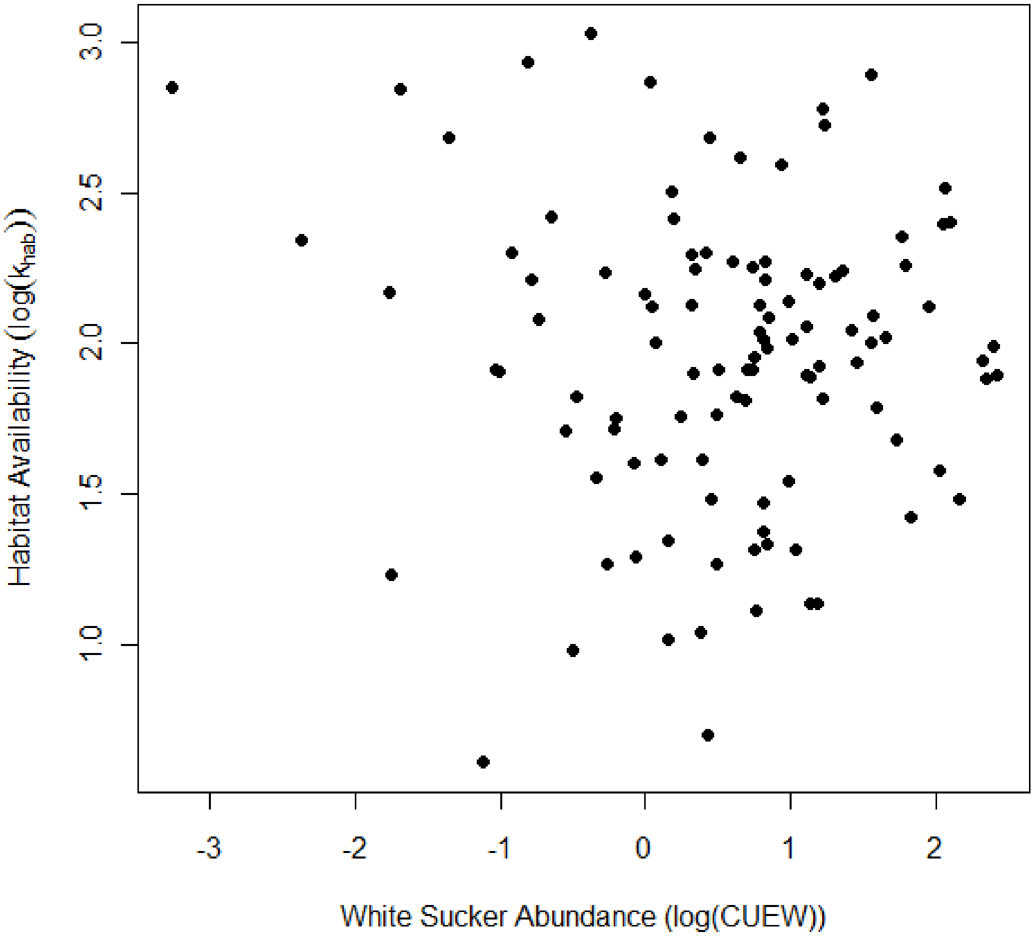

Figure 13. Correlation between white suckers CUEW (kg/ha) and index of walleye habitat (k_{hab}, kg/ha) from 107 Ontario lakes sampled using the Fall Walleye Index Netting protocol. The correlation coefficient (r = -0.05) was not statistically significant (p = 0.55).

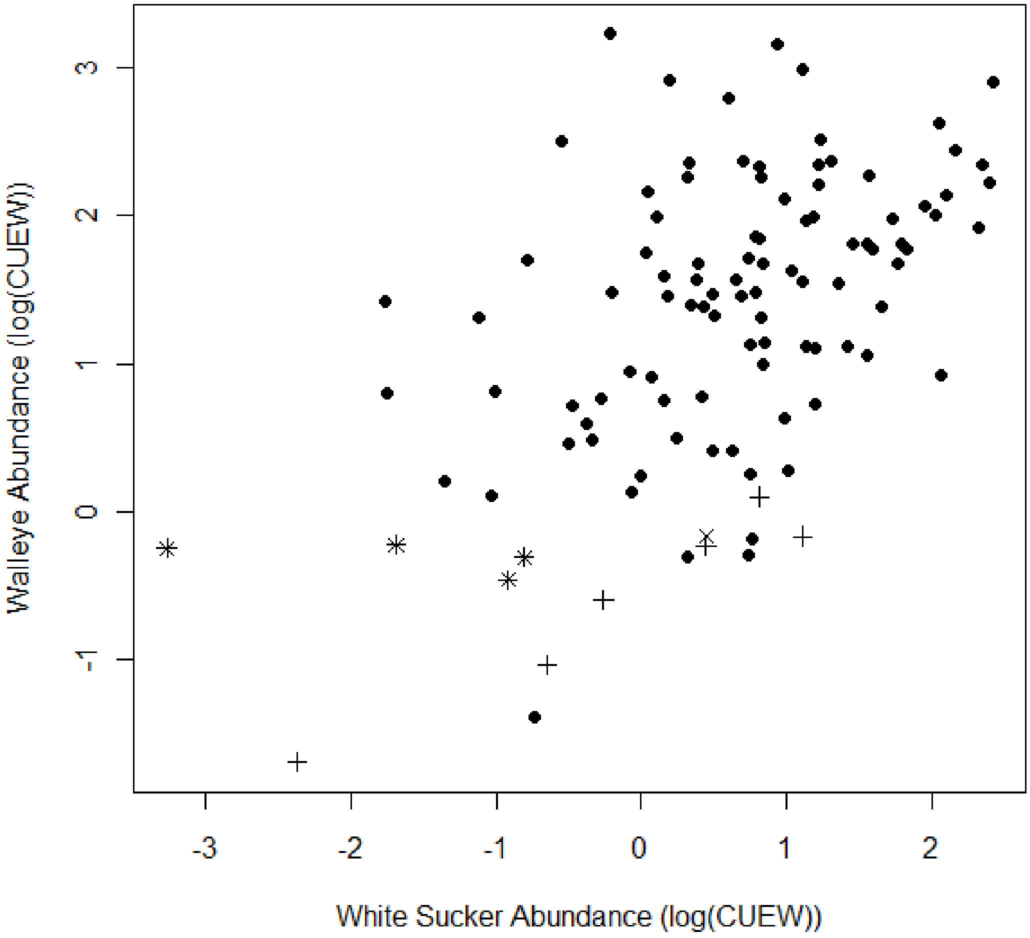

Figure 14. Correlation (r = 0.53, p<0.001) between walleye abundance (CUEW (kg/ha)) and white sucker abundance (CUEW (kg/ha)) from 107 Ontario lakes sampled using the Fall Walleye Index Netting protocol. Symbols indicate the presence of black crappie (x), bluegill (+) and both (*).

Chapter 5

Discussion

This study demonstrates how a modified Schaefer model can standardize CUEW catches to allow comparison of fish community impacts across a diverse range of habitats and fishing conditions. Previous studies have focused on controlled experiments on relatively few lakes. In contrast, the current study utilizes assessment data from many lakes (N=140) across a broad geographic area of the province of Ontario to study competition among species. It is important to recognize, however, that this approach also has some limitations. Even with high explanatory power, multiple regression results do not infer causality (James and McCulloch 1990). Patterns discerned in a descriptive analysis, such as multiple regression can, however, inform further process-related studies (Kerr and Ryder 1989).

Model results suggest that species interactions and fishing effort account for almost half (adjusted $R^2 = 0.45$) of the variation in walleye abundance not explained by physical habitat differences seen across Ontario. Fish community accounted for 19% of the variation in a subset of the data where fishing effort was not a significant predictor. The presence of bluegill, smallmouth bass and pumpkinseed were negative indicators of walleye abundance suggesting predation or a competitive interaction.

5.1 Gear Catchability

The relationship between CUEW and the true biomass is dependent on the catchability (q_{FWIN}) of the gear (Equation 12). Walleye abundance was sampled across all lakes using the standardized sampling FWIN protocol. The standardized methodology employed does not eliminate bias associated with q_{FWIN}, but theoretically holds the bias constant across surveys making data comparable (Pope *et al.* 2010). Calibration exercises for FWIN are currently being conducted (Lester pers. comm.) and should provide additional explanatory power for these results. It is important to note however that the interpretation of the effect of fishing effort and fish community, is independent of q_{FWIN}, as q_{FWIN} is retained as a variable within the model intercept.

5.2 Effect of Fishing Effort

Angler effort (E/G) was an important predictor in accounting for the differences in walleye abundance. Interestingly, the explanatory power of fishing effort was lower when lakes from zone 17were excluded. This may be a result of high effort as a result of close proximity to the most populated area of Ontario. Several factors such as travel time, trail distance and lake size have been shown to motivate angler's choice of lakes (Hunt *et al.* 2007). Accessibility (remoteness, launching facilities) and distance from urban centers is highly variable throughout Ontario, particularly throughout the north, and is likely to have a significant effect on angler distribution. Zone 17 is the smallest zone and is likely to have the most homogenous distribution of anglers. As the size of zones increase, the likelihood of fishing effort being equally distributed is reduced.

Broad scale estimates of angler effort provide limited utility in this model. One means of improving this parameter would be to incorporate effort from individual lakes. This type of data could be collected through aerial creel surveys to gauge relative effort at the lake level. Conversely, models predicting angler distribution, such as described in Hunt *et al.* (2011), could also be used to estimate how total FMZ effort is distributed between lakes.

5.3 Species Abundance Models

Models that used species CUEW as community indices did not result in any biologically relevant species interactions. There are several potential explanations that may account for this result. Similar to walleye, the abundance of other species is also likely to be affected by varying habitat across the province. Walleye abundances were standardized to the habitat model to provide catches relative to available habitat. It is noteworthy, however that species CUEW are related to physical lake features such as TDS which may account for some spurious correlations with walleye.

Angler harvest is also likely to have a confounding effect on the abundance of other species that are targeted in the recreational fishery such as smallmouth bass and northern pike. Positive correlations between walleye and other target species may simply reflect the level of overall exploitation occurring rather than any significant competitive effects between species.

The relative abundance of other species is clearly an important component of competitive interactions. In some cases, the relative abundance of different species may affect the nature of the interaction. For example, white crappie at low abundance is an important diet item for walleye, but at higher abundance have the potential to suppress walleye recruitment (Quist 2003a). Common carp (*Cyprinus carpio*) have also been shown to negatively impact centrarchid species above threshold levels of abundance (Jackson *et al.* 2010, Weber and Brown 2010). Walleye have been suspected of being limited by depensatory effects induced by rainbow smelt (Mercado-Silva *et al.* 2007). Bolby *et al.* (2010) also note depensatory effects attributed to white bass (*Morone chrsops*) and alewife (*Alosa pseudoharengus*) as factors limiting walleye abundance.

The current model assumes that species biomass will achieve or oscillate around an equilibrium state. Additional insight into complex community dynamics would be aided by examination of temporal trends within a subset of lakes. Annual contrasts in species abundance are likely to become more apparent in intensively monitored systems.

5.4 Community Assemblage

Fish communities were diverse across the Province. Multidimensional scaling results provide insight into some of the physical attributes influencing community. Axis 2 and Axis 4 were significant predictors of walleye abundance (models ORDa and ORDi) however the amount of variation explained in multiple regression models was less than that from species specific models (Table 6). This may reflect the complex relationship between environment and fish community. Secchi depth, as an indicator of water clarity, is highly correlated with Axis 4 (r=0.47). Ryder and Kerr (1989) describe light as an 'Ecological Clever' important in defining community assemblages. They provide the example that walleye are better adapted to foraging at lower light conditions than northern pike, a sympatric piscivore and that adaptation to light conditions may provide the necessary mechanism to minimize competitive interactions. Habitat suitability for species will vary across a gradient of habitat conditions, with optimal habitat for species overlapping to various degrees. It is important to consider habitat effects on species abundance when studying community interactions so as not to infer interactions that may be explained by habitat variation.

5.5 Lake Herring

The presence of lake herring was determined to be a significant positive indicator of walleye abundance. This result is consistent with the findings of Kaufman *et al.* (2006, 2009). Kaufman *et al.* (2006) found that walleye were less active, were able to maintain aerobic capacities and had increased growth potential at larger sizes when lake herring were available as prey. Differences in walleye foraging activities between lakes with lake herring and those without may also affect angler catchability. When lake herring are available as prey items, walleye tend to forage less and thus may have a reduced probability of capture by anglers (Kaufman *et al.* 2009). Increased growth potential and reduced capture in lakes with lake herring supports the findings that lake herring significantly affect walleye CUEW (α_{LaHer}= 0.3). The positive effect of lake herring may be expressed in two ways in this model. Increased growth potential may reflect reduced intraspecific competition allowing more walleye to survive to larger sizes and causing an increase in CUEW. A second potential influence of lake herring presence/absence is the indirect consequence of higher probability of angler capture in lakes where lake herring are absent (N=33). The presence of lake herring may be partially accounting for differences in exploitation rates within zones that are not captured with estimates of fishing effort derived from mail surveys. In the absence of lake herring, catchability, and thus angler catch per unit effort, is expected to increase which would likely result in higher exploitation rates.

5.6 Iowa Darters

Iowa darters (*Etheostoma exile*) were a common positive predictor of walleye abundance. Pelham *et al.* (2001) found that Johnny darters (*E. nigrum*) and to a lesser degree Iowa darters, were important diet items for age-0 walleye in Spirit Lake, Iowa (49%, 8% respectively).

Walleye predation has been shown to significantly reduce darter (both Iowa and Johnny darters) abundance although this may occur only during low densities of yellow perch which are the preferred prey item (Lyons and Magnuson 1987). The positive effect of Iowa darter in this study may be attributed to a diverse forage base reducing intraspecific competition in walleye at times when yellow perch abundance is low. It is also possible that the effect of Iowa darters may be a secondary indicator of habitat conditions as darters are intolerant of turbid waters and tend to occupy clearer waters (Scott and Crossman 1979). Darters were found in lakes with a higher mean Secchi depth and lower mean k_{hab}. This is also consistent with the MDS results as Iowa darters had a positive score on Axis 4 which is positively correlated with Secchi depth (r=0.47).

5.7 Centrarchids

Centrarchid species were largely associated with positive Axis 2 scores. The notable exception, however, was rock bass which showed little directionality on Axis 2 but was slightly negative on Axis 4. Bluegill, pumpkinseed and smallmouth bass were the centrarchid species that were significant negative predictors of walleye abundance (CUEW/ k_{hab}) in the top models. This result is consistent with predictions that centrarchid species exhibit competitive interactions with walleye.

Bluegill have been suspected predators of juvenile walleye (Schneider 1997). Evidence of predation, however, does not necessarily infer a competitive interaction since recruitment may not be affected due to a reduction in intraspecific competition. Model results suggest that walleye abundance (CUEW/ k_{hab}) will be lower in lakes where bluegill are present. This may indicate that bluegill predation on walleye fry limits walleye recruitment. Bluegill densities exceeding 50 kg/ha have been linked to walleye recruitment failure and lab studies confirmed that bluegills are effective predators of walleye at the egg and fry stages (Schneider 1997). According to Quist *et al.* (2003a), white crappies, another walleye fry predator, in high abundance could suppress walleye recruitment. Model results from the current study suggest that fry predation from bluegill is occurring at a level that negatively affects walleye abundance through recruitment.

The presence of smallmouth bass was determined to have a small but negative effect on walleye abundance across a diverse range of habitats and fish communities. This is consistent with the hypothesis that competition exists between walleye and smallmouth bass. The relatively small magnitude of the effect may be indicative of a relatively small proportion of diet overlap or of scarcity. Wuellner *et al.* (2011b) suggested that competition between walleye and smallmouth bass was mitigated by high abundance of gizzard shad, the primary prey item of both species within that study system, but not present in any of the FWIN lakes used in my analysis. Other studies have shown that smallmouth bass tend to favour crayfish whereas walleye tend to be piscivorous (Johnson and Hale 1977, Frey *et al.* 2003). Diet overlap or scarcity of prey in Ontario lakes may not occur frequently enough for smallmouth bass to greatly affect walleye abundance and thus not explain the observed relationship. Further research that incorporates relative abundance of smallmouth bass would provide additional insight into this relationship and may determine whether there is a reciprocal negative impact of walleye on smallmouth bass abundance.

The available literature suggests significant largemouth bass predation on juvenile walleye (Nate *et al.* 2003, Liao *et al.* 2004) and it was expected that largemouth bass would have a significant negative effect on walleye abundance in Ontario. However, there were few models where largemouth bass presence was a significant predictor of walleye abundance. Moreover, the effect of largemouth bass was not consistent and included both a small negative effect (α_{LmBas}=-

0.09) and a small positive effect (α_{LmBas} =0.20). These findings differ markedly from the negative correlations between largemouth bass and walleye found by Fayram *et al.* (2005a) in the smaller subset of lakes that were electrofished. There is consistency between my results however and the non-significant relationship Fayram *et al.* (2005a) found in the larger sample of lakes assessed through creel surveys. My research suggests that if largemouth bass predation is occurring on juvenile walleye, it is not at a level that is having population effects. Reduced intraspecific competition between juvenile walleye when largemouth bass predation is occurring may account for the small positive effect detected.

All centrarchid species except, longear sunfish (*Lepomis megalotis*), are found in zone 17 and it is possible that a compounding interaction with high fishing effort amplifies the individual species effect. Post *et al.* (2002) caution that depensatory effects can amplify the effects of overfishing and inhibit recovery even as harvest is reduced. Robillard and Fox (2006) only considered the piscivore guild, not potential fry predators, but considered changes over a longer period of time and determined that walleye abundance was negatively correlated with *Micropterus* sp. abundance in 4 zone 17 lakes. When index netting was conducted, zone 17 had the highest angling effort with some of the most liberal harvest regulations and greatest species diversity. It is therefore possible that the effects of high angling effort and complex fish communities have already contributed to low walleye abundance within zone 17.

5.8 White Suckers

White sucker and walleye abundance were significantly correlated ($r=0.53$, $p<0.001$). This correlation may provide additional support for the hypothesis that fry predation limits walleye recruitment. Walleye and white suckers have similar habitat preference yet white suckers are rarely harvested in the recreational fishery. Spawning habits of the two species often overlap both spatially and temporally and it is common to capture both white sucker and walleye fry in the same sampling gear (Corbett and Powles 1986). It would be expected that if angler harvest were the largest factor in determining walleye abundance, white sucker abundance would show a higher correlation with k_{hab} than with walleye abundance since white sucker abundance would be more reflective of habitat conditions. This however was not the case. It would appear that factors limiting walleye abundance act in a similar manner on white sucker populations. While causation cannot be directly inferred, lakes with the lowest abundance of both species have one or both of black crappie and bluegill present which supports a fry predation hypothesis. Further study is necessary to test the validity of the fry predation hypothesis to alternatives such as habitat alteration or another deleterious effect, such as water level manipulations (Mion *et al.* 1998), which could also be negatively affecting walleye recruitment.

5.9 Additional Considerations

An important limitation within this study may be the relatively small range that bluegill, black crappie and largemouth bass occupy in the survey. The ranges of these species in Ontario are largely confined to warmer climate areas in the south, where angling pressure also tends to be higher. Bluegill and black crappie may be acting as surrogate indicators of angling pressure and competitive interactions may not be occurring. Conversely, a more diverse fish community may provide some benefit to walleye as angling effort is likely to be distributed among more species and thus walleye may be less targeted. Effort estimates were based on total fishing effort (all species) and it is possible that targeted walleye effort and harvest will be proportionally lower in zones with more diverse fish communities.

Habitat degradation in Ontario is thought to be a major stress on walleye populations (Kerr *et al.* 1997). Changes to walleye habitat are not directly explored in this model. Future research should attempt to identify potential habitat stressors on individual lakes and include these as an additional parameter in the model. Although factors such as changes in Secchi depth following zebra mussel invasion have been incorporated into calculations of thermal-optical habitat (to the extent that available data allowed), other biotic changes may not be fully captured. Increased clarity following the invasion of zebra mussels has been shown to increase the depth of macrophyte growth in Oneida Lake which may shift production from pelagic to benthic (Zhu *et al.* 2006). Zebra mussels have also been shown to change the structure of fish, benthic, plankton and zooplankton communities (Nicholls *et al.* 2011). The impact of zebra mussels on water clarity can be incorporated into the current model but it may not fully capture the total impact on walleye populations.

5.10 Relevance to Fisheries Management

Although species introductions have historically been common practice in Ontario, especially with *Micropterus* sp., many of the ecological effects are only now becoming better understood. Climate change models for Ontario suggest that ranges for warm water species (such as bluegill and smallmouth bass) are likely to expand northward (Chu *et al.* 2005). Model results from the present study suggest that introduction, intentional or otherwise, of bluegill, pumpkinseed and smallmouth bass, and to a lesser degree black crappie, would result in a lower equilibrium biomass of walleye. The magnitude of this decline may depend on which other species are present in the fish community.

For lakes where competitors currently exist, it is unclear whether these competitor species can be managed for quality fisheries without negatively affecting walleye abundance. Results from this study were inconclusive in determining how relative abundance of potential competitors may affect walleye abundance, but do show how existing habitat models can provide a means to compare effects across a broader set of biophysical conditions. Walleye fisheries may need to be managed more cautiously in order to maintain stocks at higher levels to maintain a top predator biomass large enough to suppress potential fry predators.

5.11 Conclusions

This research provides insight into competitive interactions that may be affecting walleye abundance throughout Ontario. While the model results in isolation do not indicate causative effects, they are consistent with hypotheses supported by the literature. Centrarchid species were commonly associated with lower walleye abundance. Species that have co-evolved may have adapted niches that minimize competition. Kerr and Ryder (1989) argue that “the concept of competition is of course a contentious issue in community ecology in general, being difficult to demonstrate conclusively, perhaps because organisms go to some considerable lengths to avoid experiencing its effects”. If competitive interactions can be demonstrated within fish communities, it is expected that these would be easiest to detect when a species has been introduced.

Smallmouth bass have been introduced throughout Ontario and future studies should attempt to catalogue the introduction history. Black crappie and bluegill are relatively recent invaders in many Ontario lakes and this could explain why bluegill presence shows a strong negative effect in the current model. Further range expansion of centrarchid species, as well as the potential for other species that are not currently found in Ontario, is predicted with climate change (Chu *et al.* 2005) and could negatively affect walleye abundance and associated fisheries.

This research provides a foundation for studying how fish community changes will impact walleye. Fish community was determined to have an effect on walleye abundance. Additionally, the presence of suspected competitors predicts lower walleye abundance. While further research is required to determine how the relative abundance of competitor species affects walleye abundance fisheries management planning should consider fish community effects when establishing biological reference points for walleye.

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Appendix A

Lake Characteristics

Waterbody	FMZ	Effort (hr/ha)	Area (ha)	Secchi Depth (m)	Mean GDD (°C days)	Max. Depth (m)	Mean Depth (m)	TDS Mg/L	MSY (kg/ha)	k_{hab} (kg/ha)	Walleye CUEW (kg/net)	Number of Species
Abamategwia L.	4	6	1357.7	3.3	1406.0	33.2	9.4	26	0.51	5.54	12.23	12
Abitibi, L.	8	7	90971.7	0.3	1544.1	15.2	3.5	62	0.50	4.97	2.57	21
Agimak L.	5	11	1222.1	2.7	1630.7	15.8	3.2	19	0.63	5.91	4.20	8
Amikougami L.	8	7	359.4	1.7	1579.1	4.9	1.8	66	1.27	12.36	2.50	5
Ara L.	2	2	4926.8	5.2	1347.3	18.0	4.6	97	0.85	9.70	16.39	9
Ball L.	4	6	2915.4	1.4	1652.5	30.5	9.5	60	0.89	8.33	8.67	19
Balsam L.	17	142	4665.0	2.5	1979.2	14.9	5.0	78	1.89	14.68	0.79	20
Bark L.	15	22	3801.0	3.0	1767.0	87.5	24.3	31	0.43	3.73	1.29	16
Beak L.	5	11	524.3	3.8	1643.8	30.0	7.7	18	0.39	3.64	1.14	10
Beaverhouse L.	5	11	2000.8	5.6	1636.5	63.4	23.6	19	0.26	2.42	1.01	20
Belmont L.	17	142	758.3	5.1	2105.7	16.1	6.2	104	1.43	10.42	0.18	17
Bending L.	5	11	1135.7	2.5	1641.2	45.8	12.5	15	0.30	2.78	3.10	12
Boffin L.	5	11	544.7	4.8	1692.9	12.8	3.4	26	0.31	2.83	4.76	10
Brandy L.	15	22	104.8	1.2	1762.0	7.5	3.5	34	1.14	9.97	2.18	13
Brewer L.	5	11	102.0	1.7	1619.9	15.9	7.1	33	0.61	5.81	2.42	9
Broad L.	4	6	615.1	1.4	1616.0	5.8	2.6	70	1.68	15.97	32.93	11
Buckhorn L.	17	142	3191.0	2.9	2027.4	9.4	2.1	121	2.27	17.19	0.80	18
Burditt L.	5	11	1420.5	5.0	1672.4	23.5	9.7	60	0.54	4.93	8.52	23
Burnfield L.	7	6	113.5	3.5	1317.5	14.6	4.2	71	0.66	7.71	3.05	3
Calm L.	5	11	2480.9	3.6	1644.3	65.3	13.9	33	0.66	6.20	2.05	14
Cameron L.	17	142	1303.2	3.9	1989.6	18.3	6.3	75	1.03	8.00	0.25	14
Cecebe, L.	15	22	770.0	2.5	1781.0	19.5	4.9	29	0.82	7.04	3.08	13
Chemong L.	17	142	2280.0	2.5	2047.4	6.7	2.4	148	2.31	17.34	0.78	19
Crabs Toe	8	7	150.6	1.7	1446.2	2.5	1.1	23	0.29	3.12	3.05	7
Cuttle L.	5	11	562.5	3.1	1678.5	16.8	5.1	29	0.69	6.32	4.21	11
Departure L.	8	7	209.3	1.2	1418.5	16.0	6.1	104	1.22	13.26	3.63	10
des Mille Lacs, La.	6	3	24101.0	1.8	1511.5	24.4	6.8	33	0.83	8.42	9.54	15
Dimple L.	5	11	373.5	4.7	1638.5	25.0	12.3	18	0.21	2.01	3.98	16
Dovetail L.	5	11	794.8	3.3	1645.2	27.0	2.3	13	0.57	5.35	7.25	10
Drum L.	5	11	103.1	3.3	1642.2	17.0	4.8	14	0.32	3.03	0.84	10
Ellipse L.	4	6	177.6	3.7	1375.0	7.3	3.2	30	0.52	5.78	1.64	8
Elva L.	4	6	165.1	2.7	1595.2	5.2	1.4	31	0.33	3.19	3.30	9

Eva L.	4	6	436.0	1.8	1375.0	12.8	3.7	22	0.66	7.42	2.89	9
Expanse L.	4	6	852.1	3.1	1613.8	13.1	3.9	52	1.00	9.51	14.78	16
Factor L.	5	11	629.7	6.0	1640.8	49.4	11.9	35	0.30	2.77	4.90	12
Finlayson L.	5	11	1455.3	3.2	1648.4	51.9	16.3	65	0.72	6.73	2.26	6
Gammon L.	2	2	1218.5	3.5	1572.9	21.0	7.3	20	0.51	5.03	7.30	12
Gibson L.	15	22	263.5	2.4	1938.5	14.3	7.6	23	0.56	4.41	0.85	13
Giroux L.	15	22	115.5	1.8	1766.7	6.1	2.9	28	1.09	9.53	0.74	10
Gould L.	16	59	108.1	3.0	1955.6	8.6	1.8	186	2.24	17.59	5.73	15
Hammer L.	7	6	458.3	3.7	1332.8	11.9	3.6	51	0.66	7.56	4.01	6
Heathwalt L.	4	6	743.0	1.5	1374.0	7.6	4.8	40	0.98	11.00	7.82	13
Highbrush L.	10	21	377.5	3.5	1430.7	18.4	6.1	39	0.61	6.58	10.47	5
Husband L.	5	11	155.9	2.9	1641.8	11.6	5.1	34	0.72	6.78	10.68	10
Indian L.	4	6	3962.8	4.4	1374.0	36.0	9.4	33	0.55	6.14	9.12	15
Indian L.	10	21	1901.8	4.6	1482.0	15.5	3.9	28	0.45	4.68	1.87	8
Jacks L.	15	22	88.3	1.9	1771.1	4.0	1.1	22	1.00	8.72	1.27	5
Jones L.	5	11	389.1	1.5	1650.5	17.9	5.9	18	0.59	5.47	9.69	19
Kaopskikamak L.	5	11	1266.7	4.0	1660.5	39.0	7.2	17	0.41	3.80	2.69	18
Kapkichi L.	2	2	1277.2	2.9	1420.6	13.1	3.7	42	0.87	9.42	6.38	8
Kashwakamak L.	18	63	1219.3	5.7	2067.4	24.0	5.2	74	0.25	1.83	3.70	16
Keikewabik L.	4	6	879.4	1.9	1630.1	7.6	3.6	50	1.42	13.43	8.35	11
Kenetogami L.	8	7	158.6	2.1	1541.9	13.0	3.2	33	0.81	8.04	3.14	7
Kenorain L.	5	11	545.5	3.2	1648.2	13.7	6.1	21	0.60	5.57	25.17	7
Klotz L.	7	6	830.1	3.2	1341.5	19.8	7.8	119	1.17	13.40	23.51	11
Kukukus L.	4	6	4128.8	2.4	1623.0	19.5	5.0	31	0.93	8.78	4.13	15
Leonard L.	15	22	189.0	3.6	1744.9	18.3	6.8	25	0.11	0.94	0.60	9
Little Eye L.	5	11	75.4	2.0	1647.8	26.5	7.5	15	0.41	3.85	2.11	13
Little Turtle L.	5	11	2225.0	2.4	1663.4	9.2	3.6	18	0.84	7.80	0.92	24
Lount L.	4	6	3014.4	1.7	1690.3	32.0	7.0	47	1.04	9.47	4.02	14
Madawaska, L.	15	22	1001.1	1.5	2085.0	30.5	9.2	86	1.35	9.98	0.63	26
Mainville L.	5	11	867.7	2.3	1682.0	10.7	3.9	29	0.97	8.90	7.26	10
Manion L.	5	11	1197.9	3.3	1649.1	12.0	5.6	20	0.73	6.78	5.53	7
Manitou, L.	10	21	10460.7	7.0	1754.0	49.1	15.1	180	0.78	6.85	2.08	18
Mattagami L.	8	7	4003.1	3.3	1537.5	76.2	8.3	51	0.93	9.33	2.14	9
Mattawa L.	4	6	1730.6	3.1	1375.0	12.3	1.8	30	0.52	5.82	4.35	18
McAree L.	5	11	845.0	4.4	1619.9	37.2	12.7	28	0.48	4.59	2.66	22
Melgund L.	4	6	1201.8	3.2	1638.0	11.3	4.7	27	0.82	7.70	8.36	7
Mercutio L.	5	11	1473.1	2.8	1602.1	15.3	4.9	18	0.69	6.61	7.19	8
Michel L.	4	6	377.2	2.4	1374.0	14.3	5.4	23	0.59	6.66	18.30	6
Minisinakwa L.	8	7	1911.1	1.8	1559.4	18.3	3.3	53	1.24	12.25	4.30	8

Minnitaki L.	4	6	18087.9	2.6	1616.6	48.5	17.8	50	0.65	6.21	7.19	19
Missinaibi L.	7	6	7706.9	4.2	1411.9	94.0	19.2	55	0.68	7.39	2.47	22
Mountain L.	16	59	75.7	2.9	1969.2	3.2	1.8	130	0.77	5.99	5.85	5
Nagagami L.	7	6	5362.5	2.7	1374.7	27.5	7.5	110	1.37	15.29	12.29	6
Nagagamisis L.	7	6	2331.1	3.0	1379.5	8.1	3.8	125	1.62	18.07	6.11	8
Northern Light L.	6	3	6869.8	2.0	1487.2	39.7	8.4	27	0.65	6.70	10.59	13
Obushkong L.	8	7	437.4	2.7	1597.8	4.6	2.4	69	0.95	9.11	5.48	8
Oke L.	8	7	354.0	1.0	1435.2	3.1	1.5	22	0.70	7.51	1.31	3
Old Man L.	5	11	473.2	2.8	1591.9	26.5	13.5	35	0.35	3.43	2.23	11
Otter L.	4	6	979.0	5.8	1535.5	10.7	3.8	53	0.41	4.16	5.86	14
Otukamamoan L.	5	11	5165.8	4.7	1666.2	53.6	16.9	26	0.48	4.41	3.71	17
Pakwash L.	4	6	9825.0	1.6	1500.0	17.4	6.8	52	1.04	10.66	6.67	13
Papakomeka L.	8	7	202.3	2.0	1480.2	45.8	9.8	166	1.41	14.65	1.23	7
Partridge L.	7	6	659.5	2.8	1339.1	30.5	5.1	73	0.96	11.04	8.52	6
Patricia L.	5	11	153.7	4.2	1649.3	11.0	5.9	36	0.54	5.02	5.34	16
Pekagoning L.	5	11	1319.6	4.7	1644.1	38.4	10.6	17	0.33	3.11	7.30	25
Perch L.	5	11	703.5	2.8	1644.3	24.7	5.9	37	0.90	8.42	4.39	15
Pettit L.	5	11	1197.1	4.2	1647.8	25.0	10.6	19	0.40	3.73	5.10	9
Pigeon L.	17	142	5349.0	2.5	2015.2	17.4	3.0	121	2.47	18.83	0.73	25
Press L.	4	6	3617.9	2.7	1375.0	22.0	5.6	30	0.73	8.12	9.65	16
Quetico L.	5	11	4261.3	3.4	1634.5	61.0	13.1	18	0.48	4.52	1.89	30
Rabbit L.	11	20	2106.0	3.9	1713.6	42.7	14.2	62	0.53	4.72	1.63	11
Racine L.	7	6	1267.0	2.9	1361.0	23.5	6.0	51	0.85	9.55	6.09	7
Red L.	4	6	17676.7	2.3	1493.6	42.7	14.6	32	0.55	5.64	8.80	21
Rennie L.	7	6	579.3	4.7	1383.5	29.3	7.5	62	0.55	6.13	4.28	8
Richardson L.	5	11	148.4	3.5	1601.6	9.3	5.1	38	0.76	7.31	9.21	7
Robinson L.	5	11	420.9	6.6	1596.6	35.1	12.7	15	0.14	1.31	4.37	16
Round L.	8	7	1213.0	2.1	1588.9	36.0	17.2	72	0.41	3.95	6.32	13
Rugby L.	5	11	984.4	1.1	1641.2	7.6	3.4	53	1.38	12.93	5.96	14
Sand Point L.	5	11	3596.0	3.0	1650.5	56.1	11.6	37	0.76	7.08	4.36	31
Sandbar L.	4	6	1307.2	2.4	1375.0	13.7	6.0	44	0.94	10.56	5.35	5
Sandford L.	5	11	2921.7	7.0	1636.5	114.7	36.8	18	0.07	0.63	2.52	17
Sandstone L.	6	3	935.2	3.0	1440.2	23.8	7.3	99	0.87	9.25	10.64	9
Sandy L.	17	142	370.1	4.9	2008.7	12.8	4.8	181	2.70	20.67	1.82	15
Second Depot L.	18	63	159.6	4.2	2100.6	27.0	11.2	71	0.48	3.54	0.55	21
Selwyn L.	4	6	958.1	2.6	1334.0	9.8	1.9	31	0.59	6.76	1.12	19
Separation L.	4	6	4895.3	1.5	1677.6	35.7	6.9	50	1.06	9.69	3.72	15
Separation L.	8	7	181.4	1.8	1561.6	7.9	2.9	30	0.95	9.38	4.67	6
Seul, La.	4	6	140943.3	1.5	1621.4	47.2	9.5	60	0.96	9.15	9.52	27

Sharbot L.	18	63	1526.0	6.0	2087.7	32.0	6.5	116	0.59	4.36	1.11	19
Shikwamkwa L.	7	6	559.8	2.4	1351.7	55.8	13.7	42	0.55	6.20	1.52	9
Sideburned L.	10	21	1155.4	3.3	1430.0	8.0	1.5	52	0.41	4.41	11.48	7
Sinclair L.	8	7	947.1	3.4	1542.1	48.8	9.9	43	0.68	6.78	3.74	8
Skeleton L.	8	7	356.7	0.6	1609.2	7.0	3.1	52	1.04	9.96	0.74	6
Smoothrock L.	2	2	9824.5	2.7	1447.8	47.2	5.4	26	0.72	7.67	6.44	14
Sowden L.	4	6	3718.6	2.3	1374.0	18.3	6.3	23	0.65	7.26	5.32	9
St. Joseph, L.	2	2	51540.8	2.6	1472.9	26.2	5.1	44	1.07	11.21	18.42	20
Straw L.	5	11	427.4	2.7	1672.6	11.0	4.6	33	0.91	8.35	7.87	19
Stumpy L.	10	21	396.0	4.3	1617.2	6.7	3.2	33	0.51	4.86	7.42	3
Sturgeon L.	4	6	21412.7	4.0	1568.4	93.0	13.6	38	0.78	7.63	8.54	21
Sturgeon L.	17	142	4495.1	0.5	2008.3	12.2	2.8	85	1.47	11.27	0.35	17
Sucan L.	5	11	176.1	3.2	1673.2	16.0	3.2	63	0.76	6.98	6.82	19
Three Mile L.	15	22	354.9	4.5	1779.4	7.9	4.1	28	0.41	3.55	1.51	8
Tyrell L.	5	11	117.4	2.7	1640.5	9.3	3.2	31	0.71	6.65	4.73	8
Upper Cranberry L.	10	21	47.7	1.9	1738.0	5.5	2.2	37	1.05	9.32	0.85	9
Wakami L.	10	21	1713.0	4.4	1503.1	10.0	3.7	53	0.76	7.81	19.75	6
Wapesi L.	4	6	2366.4	1.8	1611.3	9.1	2.0	83	1.69	16.10	10.39	16
Watcomb L.	4	6	1054.5	3.9	1605.5	15.6	7.0	60	0.94	9.01	8.47	9
Wawang L.	4	6	2021.5	2.3	1545.5	26.5	6.5	25	0.70	6.94	6.11	12
Wenebegon L.	10	21	2721.4	2.1	1506.8	12.8	3.6	53	1.25	12.80	6.55	5
West Kabenung L.	7	6	1557.0	4.4	1298.8	21.3	6.4	30	0.49	5.75	4.41	6
White Otter L.	5	11	8249.0	6.5	1641.2	56.4	22.1	18	0.28	2.67	1.58	16
Whiterock L.	4	6	776.9	2.6	1599.8	9.5	3.8	38	1.06	10.16	2.60	14
Whitewater L.	2	2	10529.9	3.2	1431.0	22.9	4.6	25	0.70	7.48	10.34	14
Wildgoose L.	7	6	1737.7	4.3	1333.3	15.6	3.6	120	0.95	10.99	13.85	7
Wintering L.	4	6	1708.2	1.7	1375.0	15.9	5.3	31	0.76	8.50	8.28	14
Wintering L.	7	6	1665.2	3.2	1336.5	36.6	4.8	110	1.19	13.75	4.79	11
Wolf L.	8	7	104.7	1.9	1549.8	8.5	2.1	39	0.91	9.04	3.00	7
Young L.	4	6	804.7	2.9	1599.2	11.9	5.1	36	0.94	9.02	19.82	20

Appendix B

Determining Maximum Sustained Yield for Walleye

Lester *et al.* (2004) determined that walleye MSY could be predicted from physical lake characteristics that defined the TOHA where TOHA is defined as the area of lake bottom within the range of optimal light (8-68 lux) and temperature (11-25°C) conditions for walleye growth. TOHA is a function of climate (in determining growing season and thermocline), water clarity (as Secchi), and lake shape. The following is a summary of equations used in this study to estimate MSY for each lake. Full derivation of the equations and units are reported in Lester *et al.* (2004). Mean annual air temperature (TEMP) was estimated from annual growing degree days (GDD):

$$Temp = 17.37 \log_e GDD - 4.54 \tag{B.1}$$

Thermocline depth (z_t) for each lake was estimated using GDD, mean depth (z_{mean}) and lake area (Area) based on the analyses by Shuter *et al.* (1983) and modified by Lester *et al.* (2004).

$$z_T = 3.26\, Area^{0.109}\, z_{mean}^{0.213}\, e^{(-0.0263\, Temp)} \tag{B.2}$$

Proportion of lake above the thermocline (p_T) is 1 in non-stratified lakes or was estimated in thermally stratified lakes as:

$$p_T = 1 - \left(1 - \left(\frac{z_T}{z_{\max}}\right)^{s}\right)^{2} \tag{B.3}$$

where, z_T and z_{max} are the thermocline and maximum depths respectively and s describes the shape of the lake (Minns *et al.* 1996).

$$s = \frac{\left(3\, r + \left(r^2 + 8\, r\right)^{0.5}\right)}{4\,(1 - r)} \tag{B.4}$$

where r is determined by whether the lake thermally stratifies. For non-stratified lakes, $r=z_{mean}/z_{max}$. Where the shape of the epibenthic area is required, as in thermally stratified lakes, $r=z_E/z_T$, where z_E is the mean epibenthic depth estimated as:

$$z_E = z_T\left(1 - \frac{2}{(s+1)\left(2-\frac{z_T}{z_{\max}}\right)} + \frac{z_T^s}{(2s+1)\left(2-\frac{z_T}{z_{\max}}\right)}\right) \tag{B.5}$$

Optical habitat is maximized in each at an optimal Secchi depth that depends on lake shape and light extinction. Light extinction (k) depends on the turbidity and color of the water (Brezonik 1976, Koenings and Edmundson 1991) that accounts for the differences in light attenuation not explained solely by Secchi. For this analysis k was assumed to be a constant (k=2.3) which is within the range estimated by Lester *et al.* (2004). The relative Secchi (z_{rel}) is determined by Secchi depth, maximum depth and lake shape:

$$z_{rel} = \frac{z_{\sec}}{z_{\max}\left(1-\mathrm{e}^{-s}\right)} \tag{B.6}$$

The thermal optical habitat index (TOHAI) provides a per area index of yield rather than a whole lake (TOHA). The TOHAI estimate depends on the proportion of the lake above the thermocline (p_t) and the effect lake shape has on the optimum Secchi depth (Z_{rel}):

$$TOHAI = (GDD - 623)^{0.73} \cdot p_t \cdot z_{rel} \cdot \mathrm{e}^{-\frac{z_{rel}}{0.12\,k}} \tag{B.7}$$

Maximum sustained yield (MSY) ($kg \cdot ha^{-1} \cdot year^{-1}$) is a function of the TOHAI and total dissolved solids (TDS):

$$MSY = 0.011 \cdot TOHAI \cdot TDS^{0.534} \tag{B.8}$$

In summary, for each lake, knowing lake area (Area), mean depth (z_{mean}), maximum depth (z_{max}), Secchi depth (z_{Secchi}), GDD and TDS, allows an estimation of the MSY for walleye.

Appendix C

Top Model Summaries

MDS
all

Intercept	E/G	AXIS 1	AXIS 2	AXIS 3	AXIS 4	k	AICc	delta
-0.16	-0.04	NA	-0.36	NA	1.01	5	338.08	0.00
-0.15	-0.04	NA	-0.34	-0.30	1.01	6	338.59	0.51
-0.12	-0.04	NA	NA	NA	1.02	4	339.22	1.14
-0.11	-0.04	NA	NA	-0.32	1.02	5	339.42	1.34
-0.18	-0.04	-0.10	-0.39	NA	1.01	6	339.97	1.90
-0.17	-0.04	-0.07	-0.37	-0.29	1.01	7	340.65	2.58

MDS no17

Intercept	E/G	AXIS 1	AXIS 2	AXIS 3	AXIS 4	k	AICc	delta
-0.42	NA	NA	-0.63	-0.36	0.79	5	322.70	0.00
-0.43	NA	NA	-0.65	NA	0.78	4	322.73	0.03
-0.44	NA	-0.22	-0.69	NA	0.80	5	323.26	0.56
-0.30	-0.02	NA	-0.50	NA	0.88	5	323.58	0.88
-0.44	NA	-0.19	-0.67	-0.33	0.80	6	323.61	0.91
-0.30	-0.02	NA	-0.49	-0.34	0.87	6	323.74	1.04
-0.36	-0.01	-0.16	-0.58	NA	0.85	6	325.04	2.34
-0.35	-0.01	-0.14	-0.57	-0.33	0.85	7	325.43	2.73

CENT all

Intercept	BlCra	Blueg	E/G	LeSun	LmBas	Pumpk	RoBas	SmBas	k	AICc	delta
-0.19	NA	-1.24	-0.03	NA	NA	NA	NA	NA	4	344.18	0.00
-0.17	NA	-1.16	-0.03	NA	NA	-0.24	NA	NA	5	344.93	0.75
-0.11	NA	-1.21	-0.03	NA	NA	NA	NA	-0.17	5	344.99	0.81
-0.18	-0.34	-1.13	-0.03	NA	NA	NA	NA	NA	5	345.40	1.22
-0.15	NA	-1.17	-0.03	NA	0.36	-0.31	NA	NA	6	345.83	1.65
-0.18	NA	-1.26	-0.03	NA	0.21	NA	NA	NA	5	345.86	1.68
-0.20	NA	-1.24	-0.03	0.28	NA	NA	NA	NA	5	345.87	1.69
-0.18	NA	-1.13	-0.02	0.46	NA	-0.30	NA	NA	6	345.93	1.75
-0.09	NA	-1.24	-0.03	NA	0.29	NA	NA	-0.19	6	346.28	2.11
-0.18	NA	-1.23	-0.03	NA	NA	NA	-0.03	NA	5	346.29	2.12
-0.11	NA	-1.20	-0.03	0.37	NA	NA	NA	-0.19	6	346.35	2.18
-0.11	-0.30	-1.12	-0.03	NA	NA	NA	NA	-0.15	6	346.44	2.26
-0.12	NA	-1.16	-0.02	NA	NA	-0.18	NA	-0.12	6	346.44	2.27
-0.17	-0.25	-1.09	-0.03	NA	NA	-0.20	NA	NA	6	346.62	2.44
-0.17	-0.40	-1.14	-0.03	NA	0.28	NA	NA	NA	6	346.76	2.58
-0.17	NA	-1.16	-0.03	NA	NA	-0.24	0.01	NA	6	347.10	2.93
-0.12	NA	-1.22	-0.03	NA	NA	NA	0.03	-0.17	6	347.14	2.96
-0.09	NA	-1.16	-0.03	NA	0.39	-0.25	NA	-0.14	7	347.14	2.97
-0.19	-0.33	-1.13	-0.03	0.27	NA	NA	NA	NA	6	347.14	2.97

CENT no17

Intercept	BlCra	Blueg	E/G	LeSun	LmBas	Pumpk	RoBas	SmBas	k	AICc	delta
-0.34	-0.62	-1.60	NA	NA	NA	NA	NA	NA	4	323.25	0.00
-0.31	NA	-1.50	NA	NA	NA	-0.29	NA	NA	4	323.26	0.01
-0.35	NA	-1.74	NA	NA	NA	NA	NA	NA	3	323.32	0.07
-0.26	NA	-1.64	NA	NA	NA	NA	NA	-0.19	4	323.57	0.32
-0.26	-0.55	-1.53	NA	NA	NA	NA	NA	-0.17	5	324.00	0.75
-0.31	NA	-1.43	NA	0.48	NA	-0.36	NA	NA	5	324.15	0.89
-0.31	-0.47	-1.45	NA	NA	NA	-0.22	NA	NA	5	324.28	1.03
-0.31	NA	-1.55	NA	NA	0.28	-0.37	NA	NA	5	324.57	1.32
-0.25	NA	-1.48	NA	NA	NA	-0.22	NA	-0.14	5	324.57	1.32
-0.26	NA	-1.62	NA	0.37	NA	NA	NA	-0.22	5	324.91	1.66
-0.35	-0.68	-1.66	NA	NA	0.18	NA	NA	NA	5	325.02	1.77
-0.36	NA	-1.73	NA	0.26	NA	NA	NA	NA	4	325.04	1.79
-0.35	-0.61	-1.59	NA	0.25	NA	NA	NA	NA	5	325.04	1.79
-0.34	NA	-1.56	0.01	NA	NA	-0.32	NA	NA	5	325.26	2.01
-0.25	NA	-1.41	NA	0.52	NA	-0.29	NA	-0.15	6	325.27	2.02
-0.33	NA	-1.51	NA	NA	NA	-0.30	0.05	NA	5	325.32	2.07
-0.32	-0.53	-1.51	NA	NA	0.32	-0.30	NA	NA	6	325.32	2.07
-0.26	NA	-1.71	NA	NA	0.17	NA	NA	-0.22	5	325.35	2.10
-0.32	-0.62	-1.55	0.00	NA	NA	NA	NA	NA	5	325.35	2.10
-0.26	-0.63	-1.61	NA	NA	0.26	NA	NA	-0.20	6	325.36	2.11
-0.35	-0.63	-1.62	NA	NA	NA	NA	0.03	NA	5	325.36	2.11
-0.36	NA	-1.77	NA	NA	0.07	NA	NA	NA	4	325.38	2.13
-0.34	NA	-1.71	0.00	NA	NA	NA	NA	NA	4	325.42	2.17
-0.35	NA	-1.74	NA	NA	NA	NA	0.00	NA	4	325.45	2.20
-0.31	-0.41	-1.39	NA	0.43	NA	-0.29	NA	NA	6	325.47	2.22

-0.26	-0.53	-1.51	NA	0.35	NA	NA	NA	-0.19	6	325.48	2.23
-0.28	NA	-1.67	NA	NA	NA	NA	0.07	-0.22	5	325.54	2.29
-0.25	NA	-1.55	NA	NA	0.31	-0.30	NA	-0.16	6	325.66	2.41
-0.25	-0.46	-1.44	NA	NA	NA	-0.16	NA	-0.13	6	325.67	2.42
-0.27	NA	-1.66	0.00	NA	NA	NA	NA	-0.20	5	325.72	2.47
-0.28	-0.58	-1.56	NA	NA	NA	NA	0.09	-0.20	6	325.83	2.58
-0.32	NA	-1.48	NA	0.41	0.21	-0.41	NA	NA	6	325.85	2.60
-0.36	NA	-1.50	0.01	0.51	NA	-0.40	NA	NA	6	326.04	2.79
-0.26	-0.55	-1.53	0.00	NA	NA	NA	NA	-0.17	6	326.20	2.95

FULL

Intercept	Blueg	BnShi	E/G	IoDar	JoDar	LaHer	LmBas	LnDac	Muske	NRDac	Pumpk	RoBas	Sauge	SmBas	k	AICc	delta
-0.51	-1.11	NA	-0.02	0.34	NA	0.24	NA	NA	NA	0.42	-0.37	NA	NA	NA	8	337.91	0.00
-0.44	-1.19	NA	-0.03	0.34	NA	0.27	NA	NA	NA	0.39	NA	NA	NA	-0.26	8	337.95	0.04
-0.31	-1.11	NA	-0.03	0.36	NA	NA	NA	NA	NA	0.44	-0.38	NA	NA	NA	7	338.01	0.11
-0.44	-1.10	NA	-0.02	0.36	NA	0.26	NA	NA	NA	0.43	-0.28	NA	NA	-0.20	9	338.29	0.39
-0.47	-1.11	NA	-0.03	0.35	NA	0.26	NA	NA	NA	0.39	-0.38	NA	-0.23	NA	9	338.34	0.43
-0.44	-1.15	NA	-0.03	0.37	NA	0.28	NA	NA	NA	NA	NA	NA	NA	-0.24	7	338.38	0.47
-0.23	-1.20	NA	-0.03	0.36	NA	NA	NA	NA	NA	0.41	NA	NA	NA	-0.25	7	338.54	0.64
-0.25	-1.10	NA	-0.03	0.38	NA	NA	NA	NA	NA	0.45	-0.30	NA	NA	-0.18	8	338.67	0.76
-0.41	-1.19	NA	-0.03	0.35	NA	0.29	NA	NA	NA	0.36	NA	NA	-0.21	-0.26	9	338.69	0.78
-0.41	-1.16	NA	-0.03	0.37	NA	0.30	NA	NA	NA	NA	NA	NA	-0.23	-0.24	8	338.76	0.85
-0.51	-1.08	NA	-0.03	0.36	NA	0.26	NA	NA	NA	NA	-0.32	NA	NA	NA	7	338.76	0.85
-0.47	-1.08	NA	-0.03	0.38	NA	0.28	NA	NA	NA	NA	-0.33	NA	-0.25	NA	8	338.82	0.91
-0.27	-1.11	NA	-0.03	0.37	NA	NA	NA	NA	NA	0.42	-0.39	NA	-0.20	NA	8	338.86	0.96
-0.41	-1.10	NA	-0.03	0.37	NA	0.28	NA	NA	NA	0.40	-0.30	NA	-0.22	-0.19	10	338.88	0.97
-0.51	-1.12	NA	-0.03	0.37	NA	0.27	NA	-0.19	NA	0.45	-0.37	NA	NA	NA	9	339.15	1.24
-0.52	-1.20	NA	-0.03	0.33	NA	0.27	NA	NA	NA	NA	NA	NA	NA	NA	6	339.19	1.29
-0.30	-1.08	NA	-0.03	0.39	NA	NA	NA	NA	NA	NA	-0.32	NA	NA	NA	6	339.21	1.31
-0.53	-1.24	NA	-0.03	0.30	NA	0.25	NA	NA	NA	0.35	NA	NA	NA	NA	7	339.21	1.31
-0.22	-1.16	NA	-0.03	0.39	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.23	6	339.28	1.37
-0.45	-1.08	NA	-0.02	0.38	NA	0.27	NA	NA	NA	NA	-0.23	NA	NA	-0.19	8	339.30	1.40
-0.33	-1.24	NA	-0.03	0.33	NA	NA	NA	NA	NA	0.38	NA	NA	NA	NA	6	339.47	1.56
-0.49	-1.20	NA	-0.03	0.34	NA	0.29	NA	NA	NA	NA	NA	NA	-0.24	NA	7	339.49	1.58

-0.44	-1.20	NA	-0.03	0.36	NA	0.29	NA	-0.16	NA	0.41	NA	NA	NA	-0.25	9	339.50	1.59
-0.41	-1.08	NA	-0.03	0.39	NA	0.30	NA	NA	NA	NA	-0.25	NA	-0.24	-0.18	9	339.51	1.60
-0.20	-1.10	NA	-0.03	0.39	NA	NA	NA	NA	NA	0.43	-0.31	NA	-0.19	-0.18	9	339.66	1.76
-0.49	-1.13	NA	-0.03	0.37	-0.11	0.27	NA	NA	NA	0.42	-0.36	NA	NA	NA	9	339.67	1.76
-0.43	-1.21	NA	-0.03	0.37	-0.11	0.29	NA	NA	NA	0.39	NA	NA	NA	-0.26	9	339.68	1.77
-0.19	-1.20	NA	-0.03	0.37	NA	NA	NA	NA	NA	0.39	NA	NA	-0.18	-0.24	8	339.69	1.78
-0.31	-1.20	NA	-0.03	0.36	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5	339.74	1.83
-0.25	-1.08	NA	-0.03	0.40	NA	NA	NA	NA	NA	NA	-0.34	NA	-0.22	NA	7	339.75	1.84
-0.30	-1.12	NA	-0.03	0.39	NA	NA	NA	-0.13	NA	0.47	-0.38	NA	NA	NA	8	339.76	1.85
-0.45	-1.11	NA	-0.02	0.39	NA	0.28	NA	-0.17	NA	0.46	-0.29	NA	NA	-0.19	10	339.78	1.87
-0.30	-1.11	NA	-0.03	0.35	NA	NA	0.21	NA	NA	0.42	-0.42	NA	NA	NA	8	339.81	1.90
-0.50	-1.24	NA	-0.03	0.31	NA	0.27	NA	NA	NA	0.33	NA	NA	-0.22	NA	8	339.84	1.93
-0.50	-1.13	-0.09	-0.03	0.38	NA	0.26	NA	NA	NA	0.42	-0.37	NA	NA	NA	9	339.90	2.00
-0.44	-1.21	-0.09	-0.03	0.37	NA	0.28	NA	NA	NA	0.39	NA	NA	NA	-0.26	9	339.96	2.05
-0.48	-1.12	NA	-0.03	0.38	NA	0.29	NA	-0.16	NA	0.42	-0.38	NA	-0.21	NA	10	339.97	2.07
-0.46	-1.16	NA	-0.03	0.34	NA	0.26	NA	NA	0.23	0.42	-0.37	NA	-0.28	NA	10	340.01	2.10
-0.50	-1.09	NA	-0.02	0.34	NA	0.26	NA	NA	NA	0.41	-0.35	-0.06	NA	NA	9	340.02	2.11
-0.23	-1.08	NA	-0.03	0.41	NA	NA	NA	NA	NA	NA	-0.25	NA	NA	-0.17	7	340.03	2.13
-0.49	-1.11	NA	-0.03	0.34	NA	0.23	0.11	NA	NA	0.41	-0.39	NA	NA	NA	9	340.06	2.15
-0.43	-1.17	NA	-0.03	0.40	-0.11	0.31	NA	NA	NA	NA	NA	NA	NA	-0.24	8	340.08	2.17
-0.18	-1.16	NA	-0.03	0.40	NA	NA	NA	NA	NA	NA	NA	NA	-0.20	-0.23	7	340.12	2.21
-0.44	-1.21	NA	-0.03	0.33	NA	0.27	NA	NA	0.09	0.40	NA	NA	NA	-0.26	9	340.12	2.21
-0.50	-1.13	NA	-0.03	0.33	NA	0.24	NA	NA	0.07	0.43	-0.37	NA	NA	NA	9	340.12	2.21
-0.30	-1.12	NA	-0.03	0.38	-0.05	NA	NA	NA	NA	0.44	-0.37	NA	NA	NA	8	340.14	2.23
-0.44	-1.18	NA	-0.03	0.34	NA	0.28	NA	NA	NA	0.38	NA	-0.05	NA	-0.25	9	340.14	2.23
-0.43	-1.12	NA	-0.02	0.39	-0.10	0.28	NA	NA	NA	0.43	-0.28	NA	NA	-0.20	10	340.14	2.23
-0.31	-1.13	NA	-0.03	0.36	NA	NA	NA	NA	0.09	0.45	-0.37	NA	NA	NA	8	340.16	2.25

-0.45	-1.16	NA	-0.03	0.39	NA	0.30	NA	-0.12	NA	NA	NA	NA	NA	-0.24	8	340.21	2.30
-0.31	-1.12	-0.03	-0.03	0.38	NA	NA	NA	NA	NA	0.44	-0.38	NA	NA	NA	8	340.22	2.32
-0.43	-1.19	NA	-0.03	0.34	NA	0.26	0.03	NA	NA	0.38	NA	NA	NA	-0.26	9	340.23	2.32
-0.31	-1.11	NA	-0.03	0.36	NA	NA	NA	NA	NA	0.44	-0.38	0.00	NA	NA	8	340.26	2.36
-0.39	-1.24	NA	-0.03	0.34	NA	0.29	NA	NA	0.24	0.39	NA	NA	-0.26	-0.25	10	340.29	2.38
-0.44	-1.12	-0.09	-0.02	0.40	NA	0.28	NA	NA	NA	0.43	-0.29	NA	NA	-0.20	10	340.30	2.39
-0.22	-1.11	NA	-0.03	0.37	NA	NA	0.25	NA	NA	0.43	-0.34	NA	NA	-0.19	9	340.31	2.40
-0.42	-1.11	NA	-0.03	0.35	NA	0.24	0.15	NA	NA	0.42	-0.31	NA	NA	-0.20	10	340.38	2.48
-0.44	-1.17	-0.08	-0.03	0.40	NA	0.30	NA	NA	NA	NA	NA	NA	NA	-0.24	8	340.40	2.49
-0.51	-1.09	NA	-0.03	0.39	NA	0.29	NA	-0.15	NA	NA	-0.32	NA	NA	NA	8	340.40	2.50
-0.44	-1.13	NA	-0.03	0.37	NA	0.30	NA	NA	NA	NA	NA	-0.07	NA	-0.22	8	340.43	2.52
-0.47	-1.12	-0.07	-0.03	0.38	NA	0.28	NA	NA	NA	0.40	-0.38	NA	-0.22	NA	10	340.47	2.56
-0.27	-1.20	NA	-0.03	0.36	NA	NA	NA	NA	NA	NA	NA	NA	-0.21	NA	6	340.47	2.57
-0.49	-1.10	NA	-0.03	0.40	-0.11	0.29	NA	NA	NA	NA	-0.31	NA	NA	NA	8	340.48	2.57
-0.53	-1.25	NA	-0.03	0.33	NA	0.28	NA	-0.19	NA	0.38	NA	NA	NA	NA	8	340.48	2.57
-0.29	-1.24	NA	-0.03	0.34	NA	NA	NA	NA	NA	0.36	NA	NA	-0.19	NA	7	340.49	2.58
-0.47	-1.12	NA	-0.03	0.37	-0.06	0.28	NA	NA	NA	0.40	-0.37	NA	-0.21	NA	10	340.51	2.60
-0.25	-1.16	NA	-0.03	0.36	NA	NA	NA	NA	0.23	0.45	-0.38	NA	-0.25	NA	9	340.51	2.60
-0.22	-1.20	NA	-0.03	0.38	NA	NA	NA	-0.10	NA	0.43	NA	NA	NA	-0.24	8	340.51	2.60
-0.51	-1.15	NA	-0.03	0.34	NA	0.30	NA	NA	NA	NA	NA	-0.13	NA	NA	7	340.53	2.62
-0.46	-1.11	NA	-0.03	0.35	NA	0.25	0.11	NA	NA	0.39	-0.40	NA	-0.23	NA	10	340.53	2.62
-0.44	-1.12	NA	-0.03	0.35	NA	0.26	NA	NA	0.07	0.44	-0.28	NA	NA	-0.20	10	340.53	2.63
-0.42	-1.20	NA	-0.03	0.37	NA	0.31	NA	-0.13	NA	0.38	NA	NA	-0.19	-0.25	10	340.54	2.63
-0.43	-1.16	NA	-0.03	0.36	NA	0.27	0.09	NA	NA	NA	NA	NA	NA	-0.25	8	340.54	2.63
-0.40	-1.15	NA	-0.03	0.36	NA	0.28	NA	NA	0.23	0.43	-0.29	NA	-0.27	-0.19	11	340.58	2.68
-0.24	-1.11	NA	-0.03	0.40	NA	NA	NA	-0.11	NA	0.47	-0.30	NA	NA	-0.18	9	340.59	2.69
-0.44	-1.10	NA	-0.02	0.36	NA	0.26	NA	NA	NA	0.43	-0.28	-0.01	NA	-0.20	10	340.61	2.70

-0.44	-1.16	NA	-0.03	0.36	NA	0.28	NA	NA	0.03	NA	NA	NA	NA	-0.24	8	340.62	2.71
-0.39	-1.19	NA	-0.03	0.37	NA	0.30	NA	NA	0.18	NA	NA	NA	-0.27	-0.24	9	340.62	2.72
-0.23	-1.22	NA	-0.03	0.35	NA	NA	NA	NA	0.11	0.42	NA	NA	NA	-0.25	8	340.63	2.72
-0.22	-1.20	NA	-0.03	0.36	NA	NA	0.12	NA	NA	0.40	NA	NA	NA	-0.26	8	340.63	2.72
-0.47	-1.11	NA	-0.03	0.35	NA	0.26	NA	NA	NA	0.40	-0.38	0.01	-0.23	NA	10	340.66	2.75
-0.25	-1.11	NA	-0.03	0.36	NA	NA	0.22	NA	NA	0.40	-0.43	NA	-0.20	NA	9	340.66	2.75
-0.22	-1.20	NA	-0.03	0.38	-0.05	NA	NA	NA	NA	0.41	NA	NA	NA	-0.25	8	340.67	2.76
-0.50	-1.06	NA	-0.02	0.37	NA	0.29	NA	NA	NA	NA	-0.29	-0.08	NA	NA	8	340.67	2.76
-0.28	-1.09	NA	-0.03	0.38	NA	NA	0.27	NA	NA	NA	-0.38	NA	NA	NA	7	340.67	2.76
-0.42	-1.11	NA	-0.03	0.39	NA	0.30	NA	-0.14	NA	0.43	-0.30	NA	-0.20	-0.18	11	340.70	2.79
-0.19	-1.08	NA	-0.03	0.42	NA	NA	NA	NA	NA	NA	-0.26	NA	-0.21	-0.17	8	340.71	2.80
-0.48	-1.09	NA	-0.03	0.36	NA	0.24	0.17	NA	NA	NA	-0.35	NA	NA	NA	8	340.73	2.82
-0.51	-1.19	NA	-0.03	0.31	NA	0.29	NA	NA	NA	0.34	NA	-0.12	NA	NA	8	340.73	2.82
-0.46	-1.12	NA	-0.03	0.37	NA	0.28	NA	NA	0.17	NA	-0.33	NA	-0.29	NA	9	340.75	2.84
-0.51	-1.22	NA	-0.03	0.37	-0.12	0.30	NA	NA	NA	NA	NA	NA	NA	NA	7	340.75	2.84
-0.47	-1.09	NA	-0.03	0.39	NA	0.30	NA	-0.11	NA	NA	-0.33	NA	-0.24	NA	9	340.77	2.86
-0.23	-1.20	-0.02	-0.03	0.37	NA	NA	NA	NA	NA	0.41	NA	NA	NA	-0.25	8	340.77	2.86
-0.50	-1.10	-0.08	-0.03	0.40	NA	0.28	NA	NA	NA	NA	-0.32	NA	NA	NA	8	340.77	2.86
-0.24	-1.20	NA	-0.03	0.36	NA	NA	NA	NA	NA	0.41	NA	0.02	NA	-0.25	8	340.78	2.87
-0.53	-1.21	NA	-0.03	0.36	NA	0.29	NA	-0.15	NA	NA	NA	NA	NA	NA	7	340.79	2.88
-0.51	-1.26	NA	-0.03	0.34	-0.12	0.28	NA	NA	NA	0.35	NA	NA	NA	NA	8	340.80	2.89
-0.40	-1.20	NA	-0.03	0.37	-0.07	0.30	NA	NA	NA	0.36	NA	NA	-0.19	-0.25	10	340.80	2.90
-0.41	-1.21	-0.07	-0.03	0.38	NA	0.30	NA	NA	NA	0.36	NA	NA	-0.20	-0.26	10	340.82	2.92
-0.41	-1.16	NA	-0.03	0.39	NA	0.32	NA	-0.09	NA	NA	NA	NA	-0.22	-0.23	9	340.83	2.92
-0.24	-1.12	NA	-0.03	0.37	NA	NA	NA	NA	0.09	0.46	-0.30	NA	NA	-0.18	9	340.84	2.93
-0.26	-1.12	NA	-0.03	0.38	NA	NA	NA	NA	NA	0.46	-0.31	0.05	NA	-0.20	9	340.84	2.93
-0.44	-1.09	NA	-0.03	0.37	NA	0.27	0.16	NA	NA	NA	-0.36	NA	-0.25	NA	9	340.84	2.93

-0.23	-1.11	NA	-0.03	0.39	-0.04	NA	NA	NA	NA	0.45	-0.30	NA	NA	-0.18	9	340.86	2.95
-0.40	-1.17	NA	-0.03	0.39	-0.06	0.32	NA	NA	NA	NA	NA	NA	-0.21	-0.24	9	340.87	2.96
-0.26	-1.11	NA	-0.03	0.39	NA	NA	NA	-0.10	NA	0.44	-0.39	NA	-0.18	NA	9	340.88	2.97
-0.41	-1.17	-0.06	-0.03	0.40	NA	0.32	NA	NA	NA	NA	NA	NA	-0.22	-0.24	9	340.90	2.99

FULL no17

Intercept	Blueg	BnShi	E/G	IoDar	JoDar	LaHer	LmBas	LnDac	Muske	NRDac	Pumpk	RoBas	Sauge	SmBas	k	AICc	delta
-0.64	-1.69	NA	NA	0.35	NA	0.41	NA	NA	0.54	NA	NA	NA	-0.31	-0.28	8	314.28	0.00
-0.63	-1.53	NA	NA	0.34	NA	0.39	NA	NA	0.57	0.38	-0.32	NA	-0.31	-0.22	10	314.36	0.09
-0.65	-1.54	NA	NA	0.37	NA	0.37	NA	NA	NA	NA	NA	NA	NA	-0.28	6	314.38	0.10
-0.70	-1.52	NA	NA	0.36	NA	0.38	NA	NA	0.52	NA	-0.38	NA	-0.33	NA	8	314.43	0.15
-0.70	-1.55	NA	NA	0.32	NA	0.37	NA	NA	0.57	0.37	-0.42	NA	-0.32	NA	9	314.45	0.17
-0.63	-1.50	NA	NA	0.38	NA	0.39	NA	NA	0.53	NA	-0.28	NA	-0.32	-0.21	9	314.50	0.23
-0.65	-1.74	NA	NA	0.32	NA	0.41	NA	NA	0.57	0.33	NA	NA	-0.30	-0.29	9	314.75	0.48
-0.71	-1.38	NA	NA	0.37	NA	0.34	NA	NA	NA	NA	-0.36	NA	NA	NA	6	314.75	0.48
-0.64	-1.35	NA	NA	0.40	NA	0.35	NA	NA	NA	NA	-0.27	NA	NA	-0.21	7	314.80	0.53
-0.64	-1.37	NA	NA	0.36	NA	0.34	NA	NA	NA	0.36	-0.31	NA	NA	-0.22	8	314.89	0.62
-0.72	-1.40	NA	NA	0.34	NA	0.33	NA	NA	NA	0.35	-0.41	NA	NA	NA	7	314.98	0.70
-0.66	-1.58	NA	NA	0.34	NA	0.36	NA	NA	NA	0.31	NA	NA	NA	-0.29	7	315.03	0.75
-0.67	-1.60	NA	NA	0.35	NA	0.37	NA	NA	0.35	NA	NA	NA	NA	-0.28	7	315.09	0.82
-0.78	-1.68	NA	0.02	0.36	NA	0.46	NA	NA	0.59	NA	-0.36	NA	-0.31	-0.23	10	315.16	0.88
-0.63	-1.57	NA	NA	0.38	NA	0.39	NA	NA	NA	NA	NA	NA	-0.19	-0.27	7	315.23	0.95
-0.69	-1.40	NA	NA	0.38	NA	0.36	NA	NA	NA	NA	-0.38	NA	-0.22	NA	7	315.24	0.97
-0.66	-1.45	NA	NA	0.34	NA	0.35	NA	NA	0.38	0.40	-0.30	NA	NA	-0.22	9	315.28	1.01
-0.67	-1.66	NA	NA	0.32	NA	0.37	NA	NA	0.39	0.35	NA	NA	NA	-0.29	8	315.33	1.06
-0.77	-1.69	NA	0.02	0.33	NA	0.44	NA	NA	0.63	0.36	-0.39	NA	-0.30	-0.24	11	315.37	1.09
-0.62	-1.38	NA	NA	0.40	NA	0.37	NA	NA	NA	NA	-0.29	NA	-0.21	-0.21	8	315.42	1.14

-0.73	-1.48	NA	NA	0.32	NA	0.33	NA	NA	0.37	0.39	-0.40	NA	NA	NA	8	315.49	1.21
-0.84	-1.68	NA	0.02	0.34	NA	0.43	NA	NA	0.58	NA	-0.46	NA	-0.31	NA	9	315.50	1.23
-0.65	-1.42	NA	NA	0.38	NA	0.35	NA	NA	0.33	NA	-0.26	NA	NA	-0.22	8	315.65	1.37
-0.73	-1.44	NA	NA	0.36	NA	0.34	NA	NA	0.32	NA	-0.36	NA	NA	NA	7	315.68	1.40
-0.78	-1.50	NA	0.02	0.39	NA	0.41	NA	NA	NA	NA	-0.34	NA	NA	-0.23	8	315.74	1.46
-0.69	-1.42	NA	NA	0.35	NA	0.35	NA	NA	NA	0.33	-0.42	NA	-0.20	NA	8	315.76	1.48
-0.62	-1.39	NA	NA	0.37	NA	0.37	NA	NA	NA	0.34	-0.32	NA	-0.19	-0.21	9	315.81	1.53
-0.82	-1.69	NA	0.01	0.31	NA	0.42	NA	NA	0.61	0.35	-0.49	NA	-0.31	NA	10	315.83	1.56
-0.83	-1.63	NA	0.02	0.36	NA	0.43	NA	NA	0.42	NA	-0.35	NA	NA	-0.24	9	315.88	1.61
-0.65	-1.58	NA	NA	0.41	-0.12	0.40	NA	NA	NA	NA	NA	NA	NA	-0.27	7	315.90	1.63
-0.81	-1.64	NA	0.02	0.32	NA	0.42	NA	NA	0.46	0.37	-0.38	NA	NA	-0.24	10	315.93	1.65
-0.74	-1.83	NA	0.01	0.34	NA	0.45	NA	NA	0.57	NA	NA	NA	-0.29	-0.30	9	315.97	1.70
-0.83	-1.51	NA	0.01	0.36	NA	0.39	NA	NA	NA	NA	-0.43	NA	NA	NA	7	316.02	1.74
-0.64	-1.61	NA	NA	0.35	NA	0.39	NA	NA	NA	0.28	NA	NA	-0.18	-0.29	8	316.15	1.87
-0.73	-1.65	NA	0.01	0.36	NA	0.40	NA	NA	NA	NA	NA	NA	NA	-0.30	7	316.17	1.89
-0.66	-1.56	NA	NA	0.39	NA	0.39	NA	-0.12	NA	NA	NA	NA	NA	-0.27	7	316.18	1.91
-0.64	-1.72	NA	NA	0.38	-0.09	0.43	NA	NA	0.54	NA	NA	NA	-0.28	-0.27	9	316.19	1.91
-0.76	-1.50	NA	0.01	0.36	NA	0.40	NA	NA	NA	0.33	-0.37	NA	NA	-0.23	9	316.20	1.92
-0.77	-1.67	NA	NA	0.33	NA	0.36	NA	NA	NA	NA	NA	NA	NA	NA	5	316.21	1.94
-0.75	-1.83	NA	NA	0.30	NA	0.40	NA	NA	0.53	NA	NA	NA	-0.31	NA	7	316.23	1.96
-0.72	-1.43	NA	NA	0.37	NA	0.36	NA	-0.19	NA	0.38	-0.41	NA	NA	NA	8	316.24	1.96
-0.70	-1.43	NA	NA	0.41	-0.12	0.37	NA	NA	NA	NA	-0.36	NA	NA	NA	7	316.30	2.03
-0.72	-1.40	NA	NA	0.40	NA	0.36	NA	-0.15	NA	NA	-0.36	NA	NA	NA	7	316.33	2.06
-0.71	-1.57	NA	NA	0.34	NA	0.39	NA	-0.12	0.55	0.39	-0.42	NA	-0.30	NA	10	316.36	2.08
-0.66	-1.66	NA	NA	0.39	-0.15	0.41	NA	NA	0.38	NA	NA	NA	NA	-0.27	8	316.36	2.08
-0.88	-1.63	NA	0.02	0.34	NA	0.40	NA	NA	0.39	NA	-0.45	NA	NA	NA	8	316.39	2.12
-0.65	-1.40	NA	NA	0.39	NA	0.37	NA	-0.17	NA	0.39	-0.32	NA	NA	-0.21	9	316.41	2.13

-0.69	-1.56	NA	NA	0.38	-0.09	0.40	NA	NA	0.53	NA	-0.37	NA	-0.31	NA	9	316.41	2.13
-0.63	-1.40	NA	NA	0.43	-0.12	0.38	NA	NA	NA	NA	-0.26	NA	NA	-0.21	8	316.43	2.15
-0.63	-1.56	NA	NA	0.36	-0.08	0.40	NA	NA	0.58	0.38	-0.32	NA	-0.29	-0.22	11	316.44	2.16
-0.64	-1.54	NA	NA	0.36	NA	0.40	NA	-0.10	0.56	0.40	-0.33	NA	-0.30	-0.21	11	316.45	2.17
-0.70	-1.59	NA	NA	0.34	-0.09	0.39	NA	NA	0.57	0.37	-0.41	NA	-0.30	NA	10	316.46	2.19
-0.78	-1.77	NA	0.01	0.34	NA	0.42	NA	NA	0.40	NA	NA	NA	NA	-0.31	8	316.47	2.19
-0.66	-1.55	-0.06	NA	0.40	NA	0.38	NA	NA	NA	NA	NA	NA	NA	-0.28	7	316.47	2.20
-0.65	-1.70	NA	NA	0.36	NA	0.42	NA	-0.06	0.53	NA	NA	NA	-0.30	-0.27	9	316.49	2.21
-0.65	-1.51	NA	NA	0.37	NA	0.38	NA	NA	NA	NA	NA	-0.04	NA	-0.26	7	316.51	2.24
-0.70	-1.53	NA	NA	0.37	NA	0.39	NA	-0.08	0.51	NA	-0.38	NA	-0.32	NA	9	316.53	2.25
-0.64	-1.70	-0.03	NA	0.37	NA	0.42	NA	NA	0.53	NA	NA	NA	-0.31	-0.28	9	316.54	2.26
-0.62	-1.53	NA	NA	0.40	-0.08	0.41	NA	NA	0.54	NA	-0.28	NA	-0.30	-0.21	10	316.54	2.27
-0.82	-1.51	NA	0.01	0.33	NA	0.37	NA	NA	NA	0.33	-0.46	NA	NA	NA	8	316.56	2.28
-0.87	-1.64	NA	0.02	0.30	NA	0.39	NA	NA	0.43	0.36	-0.48	NA	NA	NA	9	316.56	2.28
-0.64	-1.68	NA	NA	0.35	NA	0.41	-0.03	NA	0.54	NA	NA	NA	-0.31	-0.27	9	316.57	2.29
-0.64	-1.69	NA	NA	0.35	NA	0.41	NA	NA	0.54	NA	NA	-0.01	-0.31	-0.28	9	316.58	2.30
-0.65	-1.37	NA	NA	0.42	NA	0.37	NA	-0.13	NA	NA	-0.27	NA	NA	-0.20	8	316.59	2.31
-0.63	-1.42	NA	NA	0.40	-0.11	0.37	NA	NA	NA	0.36	-0.30	NA	NA	-0.22	9	316.60	2.33
-0.71	-1.45	NA	NA	0.38	-0.12	0.36	NA	NA	NA	0.35	-0.40	NA	NA	NA	8	316.61	2.33
-0.65	-1.54	NA	NA	0.37	NA	0.37	0.01	NA	NA	NA	NA	NA	NA	-0.28	7	316.61	2.33
-0.63	-1.55	NA	NA	0.34	NA	0.37	NA	NA	0.57	0.39	-0.34	0.06	-0.33	-0.23	11	316.61	2.34
-0.65	-1.62	NA	NA	0.38	-0.12	0.40	NA	NA	NA	0.30	NA	NA	NA	-0.29	8	316.62	2.35
-0.66	-1.72	NA	NA	0.36	-0.15	0.41	NA	NA	0.43	0.35	NA	NA	NA	-0.29	9	316.63	2.36
-0.67	-1.61	NA	NA	0.36	NA	0.39	NA	-0.15	NA	0.33	NA	NA	NA	-0.28	8	316.64	2.36
-0.63	-1.54	-0.05	NA	0.36	NA	0.40	NA	NA	0.57	0.38	-0.33	NA	-0.31	-0.22	11	316.65	2.37
-0.69	-1.54	NA	NA	0.35	NA	0.37	0.07	NA	0.52	NA	-0.40	NA	-0.33	NA	9	316.67	2.39
-0.70	-1.53	-0.04	NA	0.37	NA	0.39	NA	NA	0.52	NA	-0.38	NA	-0.33	NA	9	316.67	2.40

-0.62	-1.52	NA	NA	0.37	NA	0.38	0.12	NA	0.53	NA	-0.31	NA	-0.32	-0.22	10	316.68	2.40
-0.64	-1.77	NA	NA	0.34	-0.10	0.43	NA	NA	0.58	0.33	NA	NA	-0.27	-0.29	10	316.69	2.41
-0.63	-1.54	NA	NA	0.34	NA	0.38	0.06	NA	0.57	0.38	-0.34	NA	-0.31	-0.22	11	316.69	2.42
-0.69	-1.51	NA	NA	0.36	NA	0.38	NA	NA	0.53	NA	-0.37	-0.02	-0.32	NA	9	316.71	2.44
-0.72	-1.85	NA	0.01	0.31	NA	0.44	NA	NA	0.60	0.31	NA	NA	-0.29	-0.31	10	316.72	2.44
-0.70	-1.56	-0.04	NA	0.34	NA	0.38	NA	NA	0.56	0.37	-0.42	NA	-0.32	NA	10	316.72	2.45
-0.65	-1.51	NA	NA	0.38	-0.14	0.39	NA	NA	0.42	0.40	-0.30	NA	NA	-0.22	10	316.72	2.45
-0.46	-1.46	NA	NA	0.42	NA	NA	NA	NA	NA	NA	-0.39	NA	NA	NA	5	316.73	2.45
-0.63	-1.50	NA	NA	0.39	NA	0.40	NA	-0.06	0.52	NA	-0.28	NA	-0.31	-0.21	10	316.74	2.46
-0.63	-1.51	-0.04	NA	0.40	NA	0.40	NA	NA	0.53	NA	-0.28	NA	-0.32	-0.21	10	316.77	2.50
-0.73	-1.50	NA	0.01	0.39	NA	0.42	NA	NA	NA	NA	-0.35	NA	-0.19	-0.22	9	316.77	2.50
-0.70	-1.35	NA	NA	0.38	NA	0.36	NA	NA	NA	NA	-0.34	-0.07	NA	NA	7	316.77	2.50
-0.70	-1.56	NA	NA	0.32	NA	0.37	0.02	NA	0.57	0.37	-0.43	NA	-0.32	NA	10	316.78	2.51
-0.63	-1.51	NA	NA	0.38	NA	0.38	NA	NA	0.53	NA	-0.29	0.04	-0.34	-0.22	10	316.79	2.51
-0.70	-1.55	NA	NA	0.32	NA	0.37	NA	NA	0.57	0.37	-0.42	-0.01	-0.32	NA	10	316.79	2.51
-0.63	-1.38	NA	NA	0.39	NA	0.34	0.15	NA	NA	NA	-0.30	NA	NA	-0.22	8	316.80	2.53
-0.71	-1.39	-0.07	NA	0.40	NA	0.35	NA	NA	NA	NA	-0.37	NA	NA	NA	7	316.83	2.55
-0.47	-1.48	NA	NA	0.38	NA	NA	NA	NA	NA	0.36	-0.43	NA	NA	NA	6	316.84	2.56
-0.72	-1.54	NA	NA	0.36	-0.14	0.37	NA	NA	0.40	0.39	-0.39	NA	NA	NA	9	316.85	2.57
-0.74	-1.50	NA	NA	0.35	NA	0.36	NA	-0.18	0.36	0.42	-0.41	NA	NA	NA	9	316.86	2.58
-0.71	-1.40	NA	NA	0.37	NA	0.33	0.10	NA	NA	NA	-0.39	NA	NA	NA	7	316.86	2.59
-0.66	-1.75	NA	NA	0.33	NA	0.42	NA	-0.09	0.56	0.34	NA	NA	-0.28	-0.29	10	316.87	2.59
-0.79	-1.51	NA	0.01	0.37	NA	0.40	NA	NA	NA	NA	-0.44	NA	-0.20	NA	8	316.87	2.60
-0.64	-1.37	-0.07	NA	0.43	NA	0.37	NA	NA	NA	NA	-0.27	NA	NA	-0.21	8	316.88	2.60
-0.67	-1.47	NA	NA	0.36	NA	0.37	NA	-0.16	0.38	0.43	-0.31	NA	NA	-0.21	10	316.91	2.63
-0.64	-1.39	-0.08	NA	0.40	NA	0.36	NA	NA	NA	0.36	-0.31	NA	NA	-0.22	9	316.98	2.71
-0.72	-1.51	NA	NA	0.40	-0.15	0.38	NA	NA	0.36	NA	-0.35	NA	NA	NA	8	316.99	2.72

-0.65	-1.71	NA	NA	0.32	NA	0.41	-0.09	NA	0.58	0.34	NA	NA	-0.30	-0.28	10	316.99	2.72
-0.67	-1.62	NA	NA	0.37	NA	0.39	NA	-0.11	0.34	NA	NA	NA	NA	-0.27	8	317.00	2.73
-0.78	-1.73	NA	NA	0.31	NA	0.36	NA	NA	0.34	NA	NA	NA	NA	NA	6	317.01	2.73
-0.74	-1.71	NA	NA	0.33	NA	0.38	NA	NA	NA	NA	NA	NA	-0.20	NA	6	317.04	2.76
-0.65	-1.48	NA	NA	0.42	-0.14	0.39	NA	NA	0.36	NA	-0.25	NA	NA	-0.21	9	317.04	2.76
-0.66	-1.56	NA	NA	0.35	NA	0.39	NA	NA	0.38	NA	NA	-0.08	NA	-0.25	8	317.04	2.77
-0.68	-1.68	NA	NA	0.34	NA	0.39	NA	-0.14	0.39	0.37	NA	NA	NA	-0.29	9	317.04	2.77
-0.76	-1.80	NA	0.01	0.30	NA	0.41	NA	NA	0.44	0.32	NA	NA	NA	-0.32	9	317.04	2.77
-0.65	-1.75	-0.04	NA	0.33	NA	0.41	NA	NA	0.57	0.33	NA	NA	-0.29	-0.29	10	317.05	2.77
-0.64	-1.34	NA	NA	0.40	NA	0.35	NA	NA	NA	NA	-0.26	-0.02	NA	-0.21	8	317.06	2.78
-0.71	-1.66	NA	0.01	0.34	NA	0.39	NA	NA	NA	0.29	NA	NA	NA	-0.30	8	317.06	2.79
-0.72	-1.42	-0.07	NA	0.37	NA	0.35	NA	NA	NA	0.35	-0.41	NA	NA	NA	8	317.07	2.79
-0.63	-1.39	NA	NA	0.36	NA	0.34	0.10	NA	NA	0.35	-0.33	NA	NA	-0.22	9	317.08	2.81
-0.65	-1.74	NA	NA	0.32	NA	0.40	NA	NA	0.57	0.33	NA	0.00	-0.30	-0.29	10	317.10	2.82
-0.69	-1.42	NA	NA	0.40	NA	0.38	NA	-0.12	NA	NA	-0.38	NA	-0.20	NA	8	317.12	2.84
-0.71	-1.38	NA	NA	0.34	NA	0.34	NA	NA	NA	0.34	-0.39	-0.05	NA	NA	8	317.13	2.86
-0.39	-1.46	NA	NA	0.41	NA	NA	NA	NA	NA	0.37	-0.34	NA	NA	-0.20	7	317.13	2.86
-0.39	-1.43	NA	NA	0.44	NA	NA	NA	NA	NA	NA	-0.30	NA	NA	-0.19	6	317.14	2.87
-0.66	-1.60	-0.06	NA	0.37	NA	0.38	NA	NA	NA	0.31	NA	NA	NA	-0.29	8	317.15	2.88
-0.76	-1.88	NA	NA	0.27	NA	0.39	NA	NA	0.56	0.28	NA	NA	-0.30	NA	8	317.17	2.89
-0.63	-1.60	NA	NA	0.40	-0.09	0.41	NA	NA	NA	NA	NA	NA	-0.17	-0.27	8	317.18	2.90
-0.39	-1.65	NA	NA	0.41	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.27	5	317.19	2.91
-0.64	-1.37	NA	NA	0.36	NA	0.34	NA	NA	NA	0.36	-0.31	0.01	NA	-0.22	9	317.20	2.92
-0.71	-1.41	NA	NA	0.34	NA	0.33	0.05	NA	NA	0.35	-0.42	NA	NA	NA	8	317.21	2.94
-0.67	-1.62	-0.06	NA	0.38	NA	0.39	NA	NA	0.35	NA	NA	NA	NA	-0.28	8	317.23	2.95
-0.66	-1.56	NA	NA	0.34	NA	0.37	NA	NA	NA	0.30	NA	-0.03	NA	-0.28	8	317.25	2.98
-0.64	-1.58	NA	NA	0.39	NA	0.40	NA	-0.09	NA	NA	NA	NA	-0.18	-0.27	8	317.26	2.98

-0.68	-1.43	NA	NA	0.40	-0.08	0.38	NA	NA	NA	NA	-0.37	NA	-0.20	NA	8	317.26	2.98
-0.77	-1.72	NA	NA	0.30	NA	0.35	NA	NA	NA	0.27	NA	NA	NA	NA	6	317.26	2.98
-0.66	-1.56	NA	NA	0.34	NA	0.37	-0.05	NA	NA	0.32	NA	NA	NA	-0.28	8	317.26	2.98
-0.69	-1.65	NA	0.01	0.37	NA	0.41	NA	NA	NA	NA	NA	NA	-0.18	-0.29	8	317.27	2.99

MGMT

Intercept	BlCra	Blueg	E/G	LaHer	LaTro	LmBas	Muske	NoPik	Sauge	SmBas	YePer	k	AICc	delta
-0.19	NA	-1.22	-0.02	NA	0.48	NA	NA	NA	NA	-0.25	NA	6	339.28	0.00
-0.36	NA	-1.21	-0.02	0.23	0.42	NA	NA	NA	NA	-0.26	NA	7	339.59	0.31
-0.28	NA	-1.26	-0.03	NA	0.42	NA	NA	NA	NA	NA	NA	5	340.24	0.96
-0.45	NA	-1.25	-0.03	0.22	0.36	NA	NA	NA	NA	NA	NA	6	340.65	1.38
-0.15	NA	-1.22	-0.02	NA	0.48	NA	NA	NA	-0.15	-0.25	NA	7	340.72	1.44
-0.33	NA	-1.22	-0.02	0.25	0.41	NA	NA	NA	-0.18	-0.25	NA	8	340.72	1.44
-0.16	NA	-1.24	-0.03	NA	0.48	0.26	NA	NA	NA	-0.28	NA	7	340.75	1.48
-0.19	-0.28	-1.13	-0.02	NA	0.48	NA	NA	NA	NA	-0.24	NA	7	340.81	1.53
0.21	NA	-1.17	-0.03	NA	0.49	NA	NA	-0.37	NA	-0.25	NA	7	340.87	1.59
0.12	NA	-1.15	-0.03	0.25	0.43	NA	NA	-0.46	NA	-0.25	NA	8	340.88	1.61
-0.36	-0.27	-1.13	-0.02	0.22	0.42	NA	NA	NA	NA	-0.24	NA	8	341.19	1.92
-0.47	NA	-1.22	-0.02	NA	0.48	NA	NA	NA	NA	-0.25	0.28	7	341.37	2.09
-0.28	-0.34	-1.15	-0.03	NA	0.42	NA	NA	NA	NA	NA	NA	6	341.43	2.15
-0.18	NA	-1.23	-0.02	NA	0.48	NA	0.06	NA	NA	-0.25	NA	7	341.43	2.16
-0.33	NA	-1.23	-0.03	0.21	0.42	0.18	NA	NA	NA	-0.27	NA	8	341.48	2.20
-0.24	NA	-1.26	-0.03	NA	0.41	NA	NA	NA	-0.16	NA	NA	6	341.53	2.25
-0.42	NA	-1.26	-0.03	0.24	0.34	NA	NA	NA	-0.19	NA	NA	7	341.62	2.34
0.16	NA	-1.21	-0.03	NA	0.43	NA	NA	-0.41	NA	NA	NA	6	341.67	2.40

0.07	NA	-1.19	-0.03	0.24	0.37	NA	NA	-0.50	NA	NA	NA	7	341.77	2.49
-0.36	NA	-1.22	-0.02	0.23	0.42	NA	0.06	NA	NA	-0.26	NA	8	341.79	2.52
0.42	NA	-1.18	-0.04	NA	0.49	0.36	NA	-0.54	NA	-0.28	NA	8	341.81	2.54
-0.47	NA	-1.21	-0.02	0.22	0.42	NA	NA	NA	NA	-0.25	0.11	8	341.82	2.54
-0.45	-0.33	-1.15	-0.02	0.22	0.36	NA	NA	NA	NA	NA	NA	7	341.92	2.64
0.17	NA	-1.16	-0.03	0.27	0.42	NA	NA	-0.48	-0.19	-0.24	NA	9	341.96	2.69
-0.16	-0.35	-1.13	-0.03	NA	0.47	0.32	NA	NA	NA	-0.27	NA	8	341.98	2.70
-0.70	NA	-1.26	-0.03	NA	0.41	NA	NA	NA	NA	NA	0.42	6	342.14	2.87
-0.28	NA	-1.27	-0.03	NA	0.41	0.15	NA	NA	NA	NA	NA	6	342.17	2.90
-0.13	NA	-1.24	-0.03	NA	0.47	0.26	NA	NA	-0.15	-0.27	NA	8	342.23	2.95

MGMT no17

Intercept	BlCra	Blueg	E/G	LaHer	LaTro	LmBas	Muske	NoPik	Sauge	SmBas	YePer	k	AICc	delta
0.18	NA	-1.47	NA	0.41	0.39	NA	NA	-0.81	NA	-0.29	NA	7	315.68	0.00
0.18	NA	-1.54	NA	0.42	0.37	NA	0.38	-0.84	NA	-0.30	NA	8	316.06	0.38
0.16	-0.59	-1.43	NA	0.42	0.36	NA	0.43	-0.82	NA	-0.27	NA	9	316.15	0.47
0.18	NA	-1.62	NA	0.45	0.34	NA	0.55	-0.81	-0.26	-0.29	NA	9	316.18	0.49
0.16	-0.52	-1.37	NA	0.41	0.39	NA	NA	-0.80	NA	-0.27	NA	8	316.22	0.54
-0.55	NA	-1.53	NA	0.32	0.39	NA	NA	NA	NA	-0.28	NA	6	316.50	0.81
0.16	-0.53	-1.51	NA	0.45	0.34	NA	0.57	-0.80	-0.23	-0.27	NA	10	316.75	1.06
-0.55	-0.54	-1.42	NA	0.32	0.38	NA	NA	NA	NA	-0.25	NA	7	316.91	1.22
-0.55	NA	-1.67	NA	0.37	0.34	NA	0.54	NA	-0.27	-0.27	NA	8	317.00	1.32
-0.58	-0.61	-1.48	NA	0.33	0.36	NA	0.41	NA	NA	-0.25	NA	8	317.04	1.36
-0.57	NA	-1.59	NA	0.33	0.37	NA	0.36	NA	NA	-0.28	NA	7	317.07	1.38
0.18	NA	-1.50	NA	0.43	0.38	NA	NA	-0.79	-0.14	-0.29	NA	8	317.23	1.55
-0.56	-0.54	-1.56	NA	0.37	0.33	NA	0.56	NA	-0.24	-0.25	NA	9	317.48	1.80
-0.01	-0.70	-1.54	NA	0.41	0.30	NA	0.43	-0.75	NA	NA	NA	8	317.67	1.98

-0.01	-0.63	-1.48	NA	0.40	0.32	NA	NA	-0.73	NA	NA	NA	7	317.71	2.03
0.19	NA	-1.52	NA	0.40	0.39	0.12	NA	-0.82	NA	-0.31	NA	8	317.76	2.08
0.14	NA	-1.63	NA	0.55	NA	NA	0.63	-0.80	-0.30	-0.24	NA	8	317.76	2.08
0.08	NA	-1.54	0.01	0.42	0.39	NA	NA	-0.76	NA	-0.30	NA	8	317.81	2.12
-0.54	NA	-1.55	NA	0.34	0.38	NA	NA	NA	-0.15	-0.27	NA	7	317.88	2.19
-0.32	NA	-1.62	NA	NA	0.48	NA	NA	NA	NA	-0.28	NA	5	317.88	2.20
0.18	-0.65	-1.50	NA	0.41	0.36	0.21	0.43	-0.83	NA	-0.29	NA	10	317.90	2.22
-0.66	-0.64	-1.51	NA	0.33	0.32	NA	NA	NA	NA	NA	NA	6	317.90	2.22
0.01	NA	-1.68	0.01	0.44	0.36	NA	0.42	-0.74	NA	-0.32	NA	9	317.93	2.25
-0.66	NA	-1.68	0.01	0.37	0.39	NA	NA	NA	NA	-0.30	NA	7	317.94	2.26
0.23	NA	-1.47	NA	0.41	0.39	NA	NA	-0.81	NA	-0.29	-0.05	8	317.95	2.26
-0.72	NA	-1.81	0.02	0.39	0.36	NA	0.43	NA	NA	-0.32	NA	8	317.96	2.28
-0.01	NA	-1.62	NA	0.40	0.32	NA	NA	-0.74	NA	NA	NA	6	317.97	2.29
0.18	-0.58	-1.43	NA	0.40	0.39	0.20	NA	-0.80	NA	-0.29	NA	9	317.99	2.31
-0.69	-0.71	-1.58	NA	0.33	0.30	NA	0.41	NA	NA	NA	NA	7	318.04	2.35
0.16	-0.48	-1.40	NA	0.42	0.38	NA	NA	-0.78	-0.11	-0.27	NA	9	318.09	2.41
-0.71	-0.58	-1.68	0.02	0.39	0.35	NA	0.47	NA	NA	-0.29	NA	9	318.15	2.46
0.01	-0.58	-1.55	0.01	0.44	0.36	NA	0.46	-0.74	NA	-0.29	NA	10	318.15	2.46
0.19	NA	-1.59	NA	0.41	0.37	0.12	0.38	-0.84	NA	-0.31	NA	9	318.18	2.49
-0.01	-0.63	-1.62	NA	0.45	0.27	NA	0.57	-0.73	-0.24	NA	NA	9	318.23	2.54
0.04	NA	-1.73	0.01	0.48	0.34	NA	0.57	-0.74	-0.25	-0.31	NA	10	318.24	2.55
-0.68	NA	-1.86	0.01	0.42	0.33	NA	0.58	NA	-0.25	-0.31	NA	9	318.24	2.55
-0.68	NA	-1.66	NA	0.32	0.32	NA	NA	NA	NA	NA	NA	5	318.24	2.56
0.13	-0.54	-1.52	NA	0.55	NA	NA	0.65	-0.79	-0.27	-0.21	NA	9	318.27	2.58
0.13	-0.61	-1.42	NA	0.52	NA	NA	0.49	-0.81	NA	-0.21	NA	8	318.33	2.64
0.53	NA	-1.62	NA	0.47	0.34	NA	0.56	-0.83	-0.28	-0.30	-0.34	10	318.33	2.64
0.26	NA	-1.54	NA	0.42	0.37	NA	0.38	-0.84	NA	-0.30	-0.08	9	318.36	2.67

-0.32	-0.53	-1.51	NA	NA	0.48	NA	NA	NA	NA	-0.25	NA	6	318.37	2.68
0.14	NA	-1.54	NA	0.52	NA	NA	0.44	-0.83	NA	-0.24	NA	7	318.39	2.71
0.19	NA	-1.65	NA	0.45	0.34	0.08	0.55	-0.82	-0.26	-0.30	NA	10	318.42	2.73
-0.01	-0.70	-1.52	NA	0.50	NA	NA	0.48	-0.76	NA	NA	NA	7	318.43	2.75
0.09	-0.51	-1.42	0.00	0.42	0.39	NA	NA	-0.75	NA	-0.28	NA	9	318.44	2.76
-0.01	-0.63	-1.61	NA	0.53	NA	NA	0.64	-0.74	-0.27	NA	NA	8	318.44	2.76
-0.67	-0.64	-1.66	NA	0.37	0.27	NA	0.56	NA	-0.25	NA	NA	8	318.45	2.76
-0.01	NA	-1.77	NA	0.45	0.27	NA	0.55	-0.74	-0.27	NA	NA	8	318.45	2.76
-0.58	NA	-1.68	NA	0.46	NA	NA	0.62	NA	-0.31	-0.22	NA	7	318.46	2.77
-0.01	NA	-1.69	NA	0.41	0.30	NA	0.37	-0.76	NA	NA	NA	7	318.47	2.78
0.22	-0.59	-1.43	NA	0.42	0.36	NA	0.43	-0.82	NA	-0.27	-0.05	10	318.49	2.81
0.19	-0.52	-1.37	NA	0.41	0.39	NA	NA	-0.80	NA	-0.27	-0.02	9	318.53	2.84
-0.65	-0.52	-1.56	0.01	0.37	0.38	NA	NA	NA	NA	-0.28	NA	8	318.55	2.86
-0.55	NA	-1.57	NA	0.31	0.39	0.11	NA	NA	NA	-0.29	NA	7	318.57	2.89
-0.01	NA	-1.76	NA	0.53	NA	NA	0.61	-0.74	-0.30	NA	NA	7	318.60	2.91
-0.33	NA	-1.69	NA	NA	0.46	NA	0.35	NA	NA	-0.28	NA	6	318.61	2.93
0.14	NA	-1.46	NA	0.51	NA	NA	NA	-0.80	NA	-0.23	NA	6	318.62	2.93
-0.54	-0.50	-1.45	NA	0.34	0.38	NA	NA	NA	-0.12	-0.25	NA	8	318.64	2.96
-0.67	-0.63	-1.65	NA	0.45	NA	NA	0.63	NA	-0.28	NA	NA	7	318.67	2.99