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BIOENERGETICS MODELING TO ASSESS AQUATIC INVASIVE SPECIES

TROPHIC IMPACT

by

Nickolas Kosmenko

A Thesis
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BIOENERGETICS MODELING TO ASSESS AQUATIC INVASIVE SPECIES

TROPHIC IMPACT

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Declaration of Co-Authorship / Previous Publication

I. Co-Authorship Declaration

I hereby declare this thesis incorporates material that is a result of joint research, as follows:

This thesis includes research that was conducted under the supervision of Dr. Timothy Johnson and Dr. Ken Drouillard, and with assistance from Dr. Christina Semeniuk. The first author was responsible for completing all analyses and interpretations, and deciding on final experimental designs. Co-authors provided guidance regarding methods, helped in the understanding of concepts, theories, and statistical procedures, and proof-read chapter drafts.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

II. Declaration of Previous Publication

This thesis includes one original paper that have been previously published/submitted for publication in a peer reviewed journal, as follows:

Thesis Chapter	Publication title/full citation	Publication status*
Chapter 2	Kosmenko, N., T. B. Johnson, K. G. Drouillard, and C. Semeniuk. In Preparation. Trophic impact comparisons between co-existing invasive and native fish species.	*In Preparation*

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ABSTRACT

Energy requirements of aquatic invasive species (AIS) relative to native species may help explain differences in trophic impact, as species requiring more energy must consume more food, depleting resources more quickly. Variables relating to energy use were compared between co-existing invasive and native fish species in invaded habitats. Most comparisons (8/12) demonstrated higher rates in invasive species (1-46% greater), suggesting high trophic impact is a characteristic of AIS and should be of consideration in management. Bioenergetic mass-balance principles indicate energy consumed by a fish is offset by metabolic (~40%), waste (~30%), and growth (~30%) demands. Since routine metabolic rate data are copious, this rate was used as a surrogate for trophic impact. Non-parametric analyses were used to find relationships between RMR and traits, creating models to predict trophic impact. The models performed poorly, yet age-at-maturity, maximum total length, and eye diameter-to-head length ratio were consistently important in describing RMR.

ACKNOWLEDGEMENTS

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freshwater (and highly anadromous), north-temperate ($\geq$ 40°N latitude) fish using four independent variables (determined important in describing RMR by random forest procedures) related to morphology and physiology. Results of validation using six fish withheld from the dataset used to train the model are shown. Validation species are placed below RMR boxes into which they were classified when run through the CT. Letters beside species' names represent actual RMR categories based on listing all 66 species in asceding order of RMR and dividing into four groups based on quartiles (A, B, C, and D). A failed classification is one in which actual species category does not match the category with the tallest bar in the box in which the species was classified, as bars represent frequency of species from the training data belonging to each category. Passing criteria was four successful classifications out of six 82

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CHAPTER 1

GENERAL INTRODUCTION

AQUATIC INVASIVE SPECIES

The term "invasive" is used when a non-native species creates negative impacts

on an invaded ecosystem. Ricciardi and Cohen (2007) linked "high impact" to species

"that have caused (either solely or in concert with other stressors) near total extirpations

of multiple native species in multiple regions". In cases where evidence was lacking,

impact was related to native species' declines post-introduction, and whether declines

were linked to an increase in the invader's population. Similarly, Ruiz *et al.* (1999)

defined ecological impact as "significant and measurable changes in the abundance or

distribution of resident species or habitats". Although the definitions vary, "impact" is

typically associated with some sort of harm and, therefore, "invasive" species are species

that cause harm.

The harm invasive species may cause includes competition, predation, parasitism,

hybridization, niche displacement and behavioural changes in native species, herbivory,

habitat change, bioturbation, toxicity, and/or the introduction of new diseases relative to

native communities (Wilson 1992; Wilcove *et al.* 1998; Ruiz *et al.* 1999). Invasive

species are considered the second-greatest cause of native species' extinctions in the

United States (Wilcove *et al.* 1998; Clavero and Garcia-Berthou 2005), having been

estimated to cost the United States $137 billion annually (Primentel *et al.* 2000; Colautti

et al. 2006). In Canada, invasive species are the sixth-leading threat to endangered

species (Venter *et al.* 2006). Although habitat loss, overexploitation, native species

interactions, natural causes, and pollution have each been shown to affect larger quantities of endangered species in Canada, invasive species still threaten a significant percentage (22%; Venter *et al.* 2006). Altogether, invasive species cost Canada between $7.5 and $35 billion per year in management expenditures and economic losses from resource declines (Dawson 2002; Colautti *et al.* 2006).

Developed countries are most active when it comes to importing invasive species, with Canada ranked ninth and the United States first (Lenzen *et al.* 2012). Leprieur *et al.* (2008) found a variety of human factors (gross domestic product, population density, percentage of urban area) may be related to non-native species richness in river basins in the Northern Hemisphere. Similarly, Marchetti *et al.* (2004) found disturbances caused by humans (mainly urbanization and water development) are common across invaded areas in California. These findings support the human activity hypothesis, which suggests habitat disruption and increased propagule pressure of non-native species, both resulting from human activities, facilitate establishment of non-native organisms (Leprieur *et al.* 2008). However, Ricciardi and Cohen (2007) report an organism's establishment and rate of spread determine only its "invasiveness", and neither component is related to the magnitude of impact. As such, the current research focuses on the impact stage only, with emphasis on Canada.

Due to the large amount of water within Canada as well as its significant coastal area, this country is considered particularly vulnerable to invasion by aquatic invasive species (AIS; CCFAM Aquatic Invasive Species Task Group 2004). Approximately three AIS become established in Canada's coastal or inland waters every two years (Ricciardi 2006), and some can have devastating effects. Sea Lamprey *Petromyzon*

marinus have established large populations in all the Laurentian Great Lakes (hereafter referred to as the Great Lakes) and have caused declines in important commercial and sport fish. The decline in top predators helped facilitate population increases in invasive Alewife *Alosa pseudoharengus* (Smith and Tibbles 1980), which preyed on young of important species such as Lake Trout *Salvelinus namaycush* (Krueger *et al.* 1995; Madenjian *et al.* 2008) and Yellow Perch *Perca flavescens* (Brandt *et al.* 1987). Further, early mortality syndrome (EMS) has resulted from thiamine deficiency in eggs of some species that consumed Alewives (Ketola *et al.* 2000; Honeyfield *et al.* 2005). Yet along with the negative impacts associated with AIS, there have also been positive impacts. Invasive Alewife and Rainbow Smelt *Osmerus mordax* have become important forage for predatory fish in the Great Lakes. Many of these predators are introduced salmonids, which are a key component of the $7 billion recreational fishery in the Great Lakes. The recently verified high incidence of naturally reproducing salmonids provides a new challenge for managers trying to balance predator demand with prey supply (Murry *et al.* 2010; Marklevitz *et al.* 2011). Collectively, billions of dollars have been spent by governments surrounding the Great Lakes on direct management (i.e. Sea Lamprey control) and stocking programs to rehabilitate and/or enhance the fisheries and ecological health of the lakes. Methods of predicting magnitude of AIS impact would be informative in management decisions, as managers would know which fish species contribute most to resource declines, and which simply coexist (or don't establish populations) in recipient environments with native species. Enhanced ability to anticipate high impact species would alleviate some of the financial- and time-related burdens of the current AIS management approach, which is largely after-the-fact.

Essington *et al.* (2001) emphasized the need for methods of predicting impact that are inexpensive and efficient, and that such methods should make use of the large variety of life-history information that has been collected for various fish species. Simon and Townsend (2003) further recommended generalizations pertaining to impacts be made across large, similar groups, as this would allow for earlier mitigation than would scrutinizing individual species. However, it is evident impact can be comprised of an array of negative effects (competition, predation, hybridization, niche displacement, changes in native species' behaviour, etc.), and although it would be helpful to have a single tool that successfully predicts overall impact of AIS relative to each other, the individual components of impact should first be better understood. An obvious starting point is trophic impact. In this research, "trophic impact" is related to food consumption and energy use only, and does not include other aspects contributing to overall impact.

Bioenergetic rates of food consumption (FCR), metabolism (MR), and growth (GR) can provide insight into magnitude of trophic impacts of AIS (Liao *et al.* 2005; Dick *et al.* 2012). Trophic impact occurs through consumption of food when an invasive species shares food resources with a native species. The greater the demand for food, the more likely competition is to occur, as it can only occur when resources are limited. Greater energy expenditure in a species through higher MR and GR increases FCR and, thus, trophic impact. As such, analyses of bioenergetic rates can help managers identify which AIS pose the greatest threat of trophic impact.

History has shown that, in many instances, fish species may be invasive in one location, but not cause harm in a different location. For example, Yellow Perch have been introduced to areas of southern British Columbia (Brown *et al.* 2009) and are now

considered a nuisance in that area of the province, yet in other areas across Canada,

Yellow perch are of no concern. Similarly, smallmouth Bass *Micropterus dolomieu* are

commonly introduced to North American inland waters as a sport fish, but depending on

the recipient ecosystem, effects of introductions can vary. For instance, Smallmouth

Bass and Walleye *Sander vitreus* may occupy similar habitats and compete for the same

food resources in many lakes (Stewart and Watkinson 2004), but due to a less

discriminant feeding style and higher tolerance for warm water, Smallmouth Bass may

thrive over Walleye in habitats with these features, yet may not do as well in cooler water

(Stewart and Watkinson 2004). Specific case-studies allow for comparison of

bioenergetic rates between invasive and native fish species and can provide insight into

why a species may be considered invasive in one area but not in another. It is expected

invasive fish species characteristically display higher FCR in order to meet higher

energetic demands of MR and GR. Information on FCR, MR, and GR may not exist for

all AIS of concern, but research has indicated these rates can be estimated by analysis of

fish traits.

Using numerous traits and food consumption data of 65 species of fish, Palomares

and Pauly (1998) generated a predictive model to estimate food consumption per unit

biomass (Q/B). One of the traits expected to correlate with Q/B was caudal fin aspect

ratio, which is defined by the formula:

$$A = h^2/s$$

where *A* is the aspect ratio, *h* is the height of the caudal fin, and *s* is the surface area of

the caudal fin. Work similar to that of Palomares and Pauly may help managers

differentiate between high- and low-trophic impact fish species. By analyzing

relationships between fish traits and FCR, MR, and GR, predictive models of trophic impact could be created that meet the criteria of Essington *et al.* (2001) and Simon and Townsend (2003): they are inexpensive, efficient, make use of available trait data, and use generalizations made across large, similar groups. The species analyzed by Palomares and Pauly (1998) included both marine and freshwater fish species from a variety of locations. To make predictive models specific to freshwater fish in Canada, there is a need to compile data for an adequate number of freshwater (or marine and highly anadromous), north-temperate fish.

RESEARCH PURPOSE AND OBJECTIVES

This research has two main objectives: 1) analyze instances of fish species invasions, examining the link between high bioenergetic rates (i.e. high trophic impact) and invasive fish species as a means to demonstrate evidence of importance of trophic impact assessment to AIS management; and 2) use the findings of the first objective combined with data on morphometric, physiologic, and ecologic traits to develop risk assessment tools to predict trophic impact of AIS relative to native species under similar environmental conditions in Canada.

METHODS TO ESTIMATE CONSUMPTION AND METABOLISM

There are different ways in which FCR and MR in fish can be estimated. Tyler (1970) found a relationship between gastric evaluation rate and amount of food in stomachs of young Cod *Gadus morhua* and suggested evacuation rate may provide insight into FCR. Eggers (1977) provided equations relating food intake to the amount of

food in the stomach as well as rate of gastric evacuation, and similarly, Persson (1982) calculated evacuation rate in Roach *Rutilus rutilus* and then used this information in a model to predict FCR (Elliott and Persson 1978). Storebakken *et al.* (1999) estimated evacuation rates of Atlantic Salmon *Salmo salar* using oxide markers and sieving of fecal matter, and mass-balance contaminant models (Trudel *et al.* 2000; Trudel *et al.* 2001) have also been used to estimate food intake. Forseth *et al.* (1992) used a radioisotope method for estimating FCR in Brown Trout *Salmo trutta* and found results agreed with those found using the method of Eggers (1977), although Forseth *et al.* (1992) stated an advantage of the radioisotope method over the methods of Eggers (1977) and Elliott and Persson (1978) was the ability to make estimations for a wider variety of fish species (i.e. those that consume larger prey).

Similar to FCR, methods of estimating MR are also varied. In addition to laboratory respirometry measurements, MR can be estimated in situ. In situ measurements have been performed on fish 3000m below surface levels (Smith 1978), and Bailey *et al.* (2002) examined an autonomous fish respirometer claimed capable of performance at depths to 6000m. Armstrong (1986) provided an equation relating heart rate to MR of Northern Pike *Esox lucius* under laboratory conditions and found changes in heart rates of Northern Pike corresponded well with changes in MRs initiated by feeding. From this finding, Armstrong (1986) suggested heart rate could also be used to estimate meal size. Lucas *et al.* (1991) used heart rate telemetry to measure MRs of Northern Pike in lochs in Scotland, and they used heart rate measurements obatined to estimate FCR. Finally, similar to using contaminant analyses to estimate FCR, MR can be estimated using chemical tracers.

A drawback of the methods mentioned here to estimate FCR and RMR is the amount of time needed to conduct each type of study. However, bioenergetic models can provide estimates of FCR and RMR from physiologic data that has already been compiled for numerous fish species, allowing researchers to make estimates without having to conduct new lab or field studies.

BIOENERGETIC MODEL

Bioenergetic models are commonly used in research (Hanson *et al.* 1997; Liao *et al.* 2005) to estimate FCR based on observed growth, or predict potential growth based on observed FCR. Hanson *et al.* (1997) provided a review of the Wisconsin Bioenergetic Model, originally developed by Kitchell *et al.* (1977) and based on mass-balance principles, where energy consumed equals energy used.

$$Consumption = Respiration + Wastes + Growth$$

The above equation can be further broken down:

$$FCR = (SMR + A + SDA) + (F + U) + (\Delta B + G)$$

where SMR is standard metabolic rate (often estimated by resting respiratory rate), A is an activity multiplier to elevate SMR to routine or active levels, SDA is specific dynamic action (the energy required to absorb and assimilate nutrients from food), F is energy used in egestion, U is energy used in excretion, ΔB is somatic growth, and G is gonad production. Mathematical equations exist to estimate FCR, respiration, and wastes based on relationships between these components and fish weight, diet, and water temperature. Once these rates have been estimated, growth can be calculated by subtracting energy used through respiration and wastes from FCR.

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In general, specific rates of FCR and respiration decrease with fish weight when temperature is held constant (Figures 1.1 and 1.2). When weight is constant and temperature varies, FCR and respiration increase to maximum values, then decline thereafter, with an exception being the exponential form of the temperature-dependent function for both FCR and respiration (Stewart *et al.* 1983; Figures 1.3 and 1.4). Although these general patterns are consistent for all fish, the rates of increase and decrease, as well as the maximum values and intercepts vary between fish species as well as between life stages within species. As such, researchers have developed unique parameter values allowing differentiation of bioenergetic rates between species and life stages within species. Use of these parameter values has been widespread, facilitated through the popular *Fish Bioenergetics* software (Hanson *et al.* 1997), and evaluation of parameter values is on-going. For instance, Rice and Cochran (1984) evaluated a bioenergetics model for Largemouth Bass *Micropterus salmoides* published a year earlier (Rice *et al.* 1983) and found it performed well. Bajer *et al.* (2003) evaluated performance of two bioenergetics models (Karas and Thoresson 1992; Hanson *et al.* 1997) applied to Yellow Perch and found neither model predicted SMR or growth well. Madenjian *et al.* (2006) evaluated performance of a general coregonid bioenergetics model developed by Rudstam *et al.* (1994), applying it to Lake Whitefish *Coregonus clupeaformis*. Madenjian *et al.* (2006) found the model overestimated FCR and underestimated growth. The continued evaluation of bioenergetics models through studies such as those mentioned here facilitates increased confidence when models are applied to fisheries management. By comparing estimates of bioenergetic rates between species, researchers can determine which require more energy for daily processes and, hence, must consume

the most food. In this way, rates of resource depletion, or trophic impact, can be

predicted for species of concern.
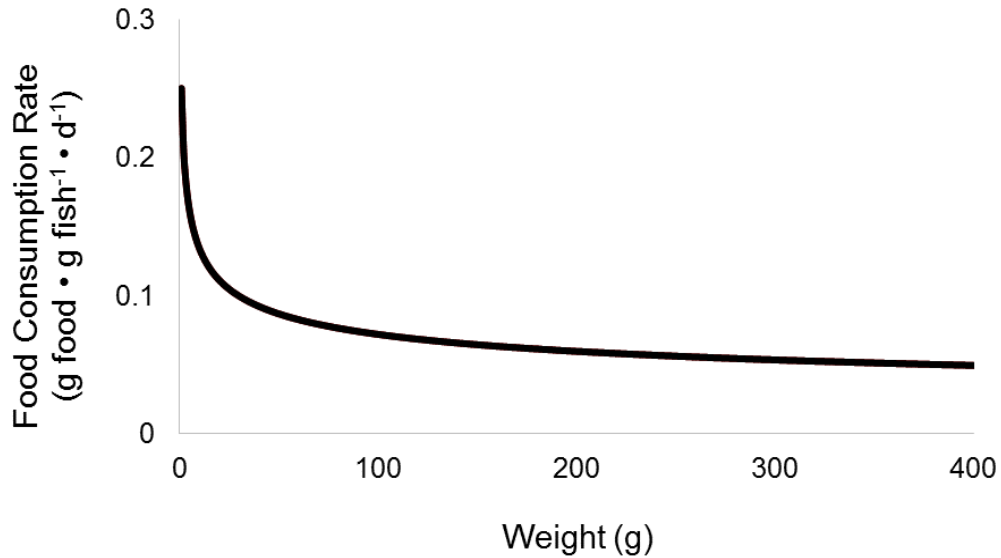
Figure 1.1. Maximum food consumption rate of a Yellow Perch *Perca flavescens* at 23°C (Kitchell *et al.* 1977).
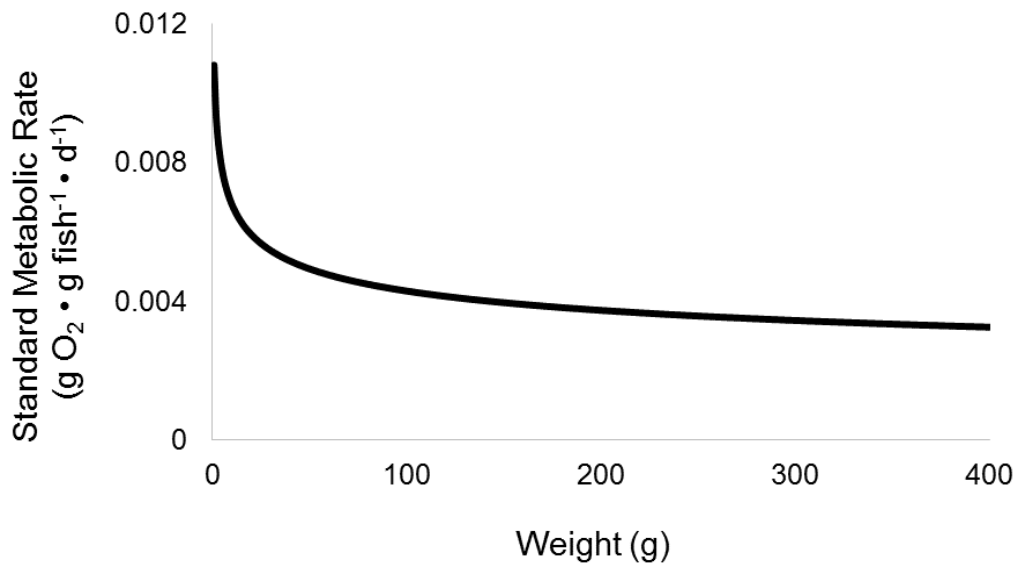
Figure 1.2. Standard metabolic rate of a Yellow Perch *Perca flavescens* at 23°C (Kitchell *et al.* 1977).
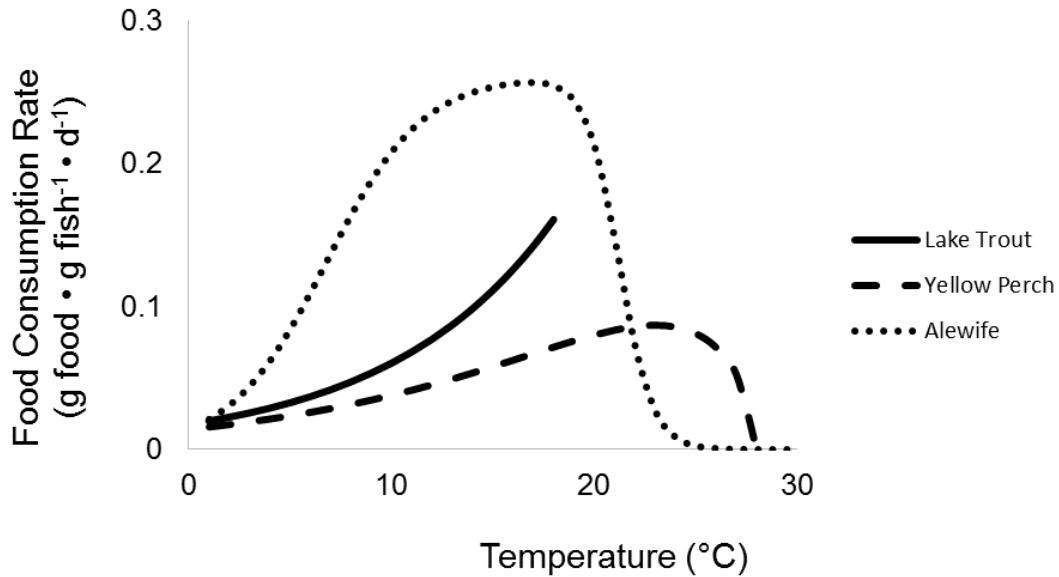
Figure 1.3 Maximum food consumption rates of a 50g Lake Trout *Salvelinus namaycush* (Stewart *et al.* 1983), a 50g Yellow Perch *Perca flavescens* (Kitchell *et al.* 1977), and a 50g Alewife *Alosa pseudoharengus* (Stewart and Binkowski 1986).
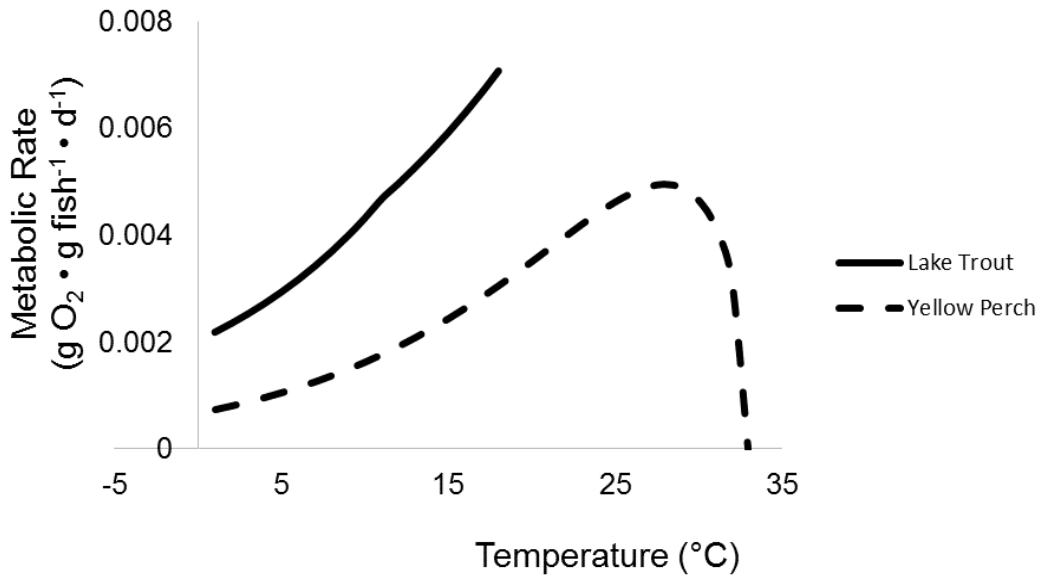
Figure 1.4. Routine metabolic rates of a 50g Lake Trout *Salvelinus namaycush* (Stewart *et al.* 1983), a 50g Yellow Perch *Perca flavescens* (Kitchell *et al.* 1977), and a 50g Alewife *Alosa pseudoharengus* (Stewart and Binkowski 1986).

The current research relies most heavily on the respiration component of the

mass-balance equation. Respiromentry experiments provide data on how much oxygen a

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fish consumes at various weights and temperatures and at various levels of activity. Activity of fish may vary from completely resting, to spontaneous bursts, to sustained swimming, to active. Correspondingly, oxygen consumption rates, or MRs of fish are classified as either standard (sometimes called resting, SMR), routine (RMR), which can be used to predict MR of fish in field situations, as it adds spontaneous activity to SMR (Beamish and Mookherjii 1964), or active, which occurs when fish are exercised (spawning migrations, pursuit of prey, escape from predators, etc.). Fish are fasted prior to typical respirometry experiments to limit effects of SDA on MR, so although the respirometry component of the mass-balance equation includes SDA, Chapter 3 of the current research does not include effects of this component. However, parameter values for SDA are very similar among fish species (~15-18% of total metabolic costs) and, therefore, would not provide much help in differentiating between RMRs.

A drawback of using bioenergetic parameter values to estimate field MR is the differing conditions between lab and field settings. RMRs also vary from one field setting to another, as fish in one location may be exposed to different levels of certain stimuli than the same species of fish in another location. The variety of conditions across a species' range would necessitate the need for large amounts of in-situ study to quantify RMR under various scenarios. Lab settings provide environments where external stimuli can be controlled, allowing for consistency between studies. However, researchers must be cognizant of the various factors that may confound MR measures (Brett 1962). The ability to compare measures from different studies or trials within studies will be negatively affected if such factors as temperature, salinity, and oxygen content vary, or if fish are insufficiently fasted (Brett 1962) or fasted for unequal durations. Further, often

instead of determining whole new parameter sets for fish species, researchers borrow values from similar species, which reduces the opportunity for parameter sets to adequately demonstrate how species differ in terms of bioenergetic rates. However, despite these shortcomings, bioenergetic analyses have been important in many fisheries applications (Hansen *et al.* 1993; Ney 1993; Ney 1995; Kitchell *et al.* 2005; Chipps and Wahl 2008; Hartman and Kitchell 2008).

Using bioenergetic analyses to develop decision support tools is not a new idea. As previously mentioned, Palomares and Pauly (1998) used multiple regression analyses to find relationships between fish traits and Q/B to help improve estimates used in trophic ecosystem modelling. Kolar and Lodge (2002) also developed decision support tools, but specifically targeted at AIS management. Their work involved using discriminant analysis and classification tree (CT) analysis to develop tools to predict success at various stages of invasion for potential invasive fish in the Great Lakes. Similarly, Mercado-Silva *et al.* (2006) used CT analysis to predict the spread of Rainbow Smelt *Osmerus mordax* in Ontario, Wisconsin, and northern Maine. To develop their tools, Kolar and Lodge (2002) and Mercado-Silva *et al.* (2006) relied on case-specific study. Kolar and Lodge (2002) looked at species already present in the Great Lakes for insight into which traits may discriminate between success and failure at the establishment and spread stages of invasion in the area. Mercado-Silver *et al.* (2006) used data from lakes in southern Maine containing native populations of Rainbow Smelt to get an idea of habitat preference. The strength of the research conducted by Kolar and Lodge (2002) was that it made use of data collected specifically from the area to which the decision support tools were to be applied. The work of Mercado-Silva *et al.* (2006) also had some

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specificity in that locations from which data had been collected were geographically in close proximity to locations to which the decision-support tool was to be applied. By using already existing data, both research teams did not have to perform their own experiments to determine relationships to inform their tools. In ecology, using case-studies to inform decision-support tools is not only more efficient than conducting new experiments, but is also necessary in many cases. It simply does not make sense to purposefully introduce new species to novel ecosystems to help develop decision-support tools to combat AIS invasion. As well, lab studies lack the complex interactions of natural systems and, therefore, may not provide accurate estimates of what may take place in field scenarios. For these reasons, the current research relies on case-specific studies to meet its first objective (Chapter 2) prior to proceeding to the second objective (Chapter 3).

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CHAPTER 2[1]

TROPHIC IMPACT COMPARISONS BETWEEN CO-EXISTING INVASIVE AND

NATIVE FISH SPECIES

INTRODUCTION

Canada is vulnerable to introductions of aquatic invasive species (AIS) because of

the country's long coastline and numerous aquatic environments. Such characteristics

make the detection and management of AIS within the country a top priority (CCFAM

Aquatic Invasive Species Task Group 2004). Collectively, AIS cost the Canadian

economy between \$7.5 and \$35 billion annually (Dawson 2002; Colautti *et al.* 2006).

Research indicates approximately three AIS become established in Canada's coastal or

inland waters every two years (Ricciardi 2006), and although some do not contribute

much to resource declines, others have had significant impacts.

Analyzing invaded habitats and the resident biota is essential in AIS management

(Olden *et al.* 2006). Some non-native fish may have an impact in one area, but may be of

no concern relative to other species in another location where species composition and/or

habitat (climate, substrate, temperature) is different. An example of this dichotomy is

invasive Yellow Perch *Perca flavescens* in southern British Columbia (BC). Yellow

Perch are common to many areas of North America (Scott and Crossman 1973), where

they are typically thought of as an innocuous representative of the ecosystem within

which they exist. After a history including both legal and illegal introductions (Brown *et al.* 2009; Runciman and Leaf 2009), Yellow Perch are now a management concern in southern BC. Introductions of Yellow Perch have been shown to affect growth and feeding habits of some salmonid species (Fraser 1978), hence efforts are now underway to reduce impact on important salmonid fisheries. Invasive Rainbow Smelt *Osmerus mordax* in various North American waters has also attracted management attention. Evans and Loftus (1987) suggested Rainbow Smelt may have harmful, neutral, or even beneficial effects on other species in the Laurentian Great Lakes region (hereafter referred to as the Great Lakes). Rainbow Smelt are a significant prey of Walleye *Sander vitreus* and Sauger *Sander canadensis* in Lake Winnipeg, but may cause increases in mercury content and reduced eating quality in such predatory fish (Stewart and Watkinson 2004). As well, Rainbow Smelt have been shown to prey on young of, as well as compete with other fish species (Loftus and Hulsman 1986; Hrabik *et al.* 1998; Hrabik *et al.* 2001).

The Great Lakes themselves provide an excellent opportunity to study effects of numerous AIS due to a long history of introductions, including both intentional and unintentional activities (Mills *et al.* 1994). Over the past two centuries, over 25 non-native species have been introduced to the Great Lakes (Mills *et al.* 1993; Ricciardi 2006; US Environmental Protection Agency 2011). Within these waters, introductions have been both harmful and beneficial. Perhaps the most famous harmful introductions include Sea Lamprey *Petromyzon marinus*, which has parasitized economically important species in the Great Lakes, and dreissenid mussels (Zebra Mussels *Dreissena polymorpha* and *D. bugensis*), which have changed nutrient dynamics and water quality (Heath *et al.*

1995), altered benthic invertebrate communities (Botts *et al.* 1996), increased mortality of

native mussels (Haag *et al.* 1993), and biofouled drinking water- and hydro-electric

facilities (Connelly *et al.* 2007). Beneficial introductions include those related to sport

fishing, and although there is no doubt sport fish have some impact on ecosystem

functioning, the economic value associated with these introduced species has been

welcomed. Sport fishing in the Great Lakes is valued at $7 billion annually (American

Sport Fishing Association 2008; Dettmers *et al.* 2012), and many of the salmonid species

angled for are non-native, such as Chinook Salmon *Oncorhynchus tshawytscha*, Coho

Salmon *Oncorhynchus kisutch*, Rainbow Trout *Oncorhynchus mykiss*, Pink Salmon

Oncorhynchus gorbuscha, Sockeye Salmon *Oncorhynchus nerka*, Atlantic Salmon *Salmo

salar*, and Brown Trout *Salmo trutta*. The range of impact, including differing

perspectives from different user groups (Dettmers *et al.* 2012), highlights the complexity

of AIS management, helping to explain why it is difficult to predict which species may be

beneficial or have no significant impacts, and which may cause harm.

Ecological impact of AIS can take many forms: physical alteration of structure

(Connelly *et al.* 2007), shifts in chemical processes (Heath *et al.* 1995), increases in

mortality through predation (Sepulveda *et al.* 2013) or fouling (Haag *et al.* 1993), and/or

trophic impact (Wilson *et al.* 2004) which is the focus of this research. Trophic impact

can be assessed through analysis of food consumption rate (FCR; Liao *et al.* 2005; Dick

et al. 2012), as species that consume more food relative to others will deplete resources

more quickly. Reduction in populations of co-habiting species can lead to alterations in

energy pathways, including trophic cascades (Simon and Townsend 2003). Bioenergetic

mass-balance models (Winberg 1956; Kitchell *et al.* 1977; Hanson *et al.* 1997) are a

popular approach to estimate the energetic requirements of fishes. The mass-balance

approach explores the difference between gains through FCR and the energetic costs of

metabolism and wastes under specified growth and thermal conditions; gains in excess of

costs are available for growth.

$$Consumption = Metabolism + Wastes + Growth$$

Metabolism is expressed as routine metabolic rate (RMR) which consists of the

standard metabolic rate for a resting fish and an activity multiplier to account for normal

spontaneous activity (Beamish and Mookherjii 1964). Specific dynamic action (SDA), or

the cost of digesting and assimilating food, is also considered part of the metabolic cost.

Wastes include egestion and excretion, while growth considers both somatic and gonadal

production. Brett and Groves (1979) found that approximately 37-44% of ingested

energy is used for metabolism, 27-43% is used for egestion and excretion, and 20-29% is

available for growth. Therefore, understanding one or more of the bioenergetic processes

of food consumption, metabolic rate, or growth may provide an approximation of the

trophic impact of a species.

The hypothesis of the current research is that energetic rates, and therefore trophic

impact, will be higher in invasive compared to native fish species. This hypothesis was

tested using bioenergetic principles in two ways: 1) provide and compare measures of

FCR, RMR, and GR of invasive and co-existing native fish species based on actual

scenarios, and 2) summarize actual scenarios that evaluated one or more of FCR, RMR,

and/or GR in invasive compared to co-existing native fish species. To differentiate

between the studies used in objectives 1 and 2, studies used in the first objective were

termed "case-histories", while studies used in the second objective were termed "case-studies".

METHODS

Bioenergetic rates for a species can vary greatly from one location to another in response to environmental variables such as temperature, water current, amount of habitat available for hiding from predators, interactions with other species, abundances and types of prey, etc. For instance, reduced growth occurs in species such as Northern Pike *Esox lucius* (Margenau *et al.* 1998), Yellow Perch (Heath and Roff 1996), and Coho Salmon (Rosenfeld 2005) in areas where these species exist in high densities and/or feed on nutritionally poor food. As well, oxygen consumption rate is typically elevated in fish inhabiting streams as opposed to calm water (Clausen 1936). As such, the current research uses case-specific scenarios and generally does not make comparisons between bioenergetic rates of species across scenarios.

For the first objective, literature was reviewed for scenarios in which invasive and native fish species demonstrated trophic overlap (i.e. shared food resources). Bioenergetic rates for each species were determined using four pieces of information upon which energy use in a species depends: 1) species weight, 2) water temperature, 3) species diet including prey energy densities, and 4) predator energy density. Allometric principles (Peters 1983) reveal that FCR and RMR decrease with increasing body size (Kleiber 1932; Hanson *et al.* 1997). Additionally, thermodynamic principles suggest FCR and RMR increase with increasing temperature up to the species-specific physiological maximum, after which mortality quickly ensues (Hanson *et al.* 1997;

Gillooly *et al.* 2001). The nutritional composition of a species' diet can cause large differences in GR potential between two separate species, although in the current research this component was expected not to account for much difference since a requirement of scenarios analyzed was evidence of trophic overlap. Lastly, energy density of the species is used to convert growth from units of energy ($J \cdot g\ fish^{-1} \cdot d^{-1}$) to units of mass ($g\ fish\ mass \cdot day^{-1}$). Body weight of each species was set based on information provided by the case-histories examined. Water temperatures were either based on the temperatures provided by the case-histories, or in the absence of temperature information, was set to the average final temperature preferendum (FTP) of the invasive and native species examined. Diet of each species was based on information provided by the case-histories, and prey and predator energy densities were obtained from literature.

The first bioenergetic rate calculated for each species was FCR. For simplicity, it was assumed the maximum proportion of food consumption was being met in each scenario (i.e. bioenergetics p = 1), meaning no environmental factors were assumed to be limiting FCR other than water temperature. This assumption made for conservative estimates of differences between bioenergetic rates, since in scenarios involving competition, resources are limiting and, thus, the negatively affected (i.e. non-invasive) species should demonstrate reduced FCR. FCR was expressed as $g\ food \cdot g\ fish^{-1} \cdot d^{-1}$ for graphical display, but needed to be converted to $J \cdot g\ fish^{-1} \cdot d^{-1}$ for later use in the calculation of GR. Conversion from the former to the later units was achieved by multiplying FCR by prey energy density ($J \cdot g\ prey^{-1}$). RMR, including SDA and activity, was similarly expressed in units of $g\ O_2 \cdot g\ fish^{-1} \cdot d^{-1}$ for graphical display, but was converted to $J \cdot g\ fish^{-1} \cdot d^{-1}$ for later use in calculating GR. This conversion was

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achieved by multiplying RMR by the oxy caloric coefficient of 13,562 J • g oxygen^{-1}.

Energy used in egestion and excretion was converted from g waste • g fish^{-1} • d^{-1} to J • g

fish^{-1} • d^{-1}, again for later use in calculating GR, by multiplying by prey energy density.

Lastly, GR was calculated by subtracting energy allocated to RMR and wastes from FCR.

GR was then converted to g fish mass • g fish^{-1} • d^{-1} to standardize for differences in body

mass among species.

Similar to the first objective, for objective 2, literature was reviewed for scenarios

in which invasive and native fish species demonstrated trophic overlap (i.e. shared food

resources). However, instead of calculating bioenergetic rates, the scenarios were simply

searched for some form of evaluation of FCR, RMR, or GR in the invasive and native

fish species.

The literature search conducted increased awareness of how difficult a task it is to

find either 1) studies providing evidence of substantial trophic overlap between native

and invasive fish species as well as providing enough information to estimate FCR, RMR

and GR in the case of case-histories, or 2) studies providing evidence of substantial

trophic overlap between native and invasive fish species and simply providing some form

of evaluation of bioenergetic rates in both species groups. Quantification of the number

of useful versus non-useful studies encountered in the current research would help

convey the tedious nature of this sort of research, thereby supporting suggestions

concerning improvements that could be made to studies examining interactions between

native and invasive fish species. Since the literature search performed in the current

research was not documented, a follow-up search comprised of three parts was performed

using Web of Science. The first two parts were targeted at specific species while the

third part was targeted at a specific lake. This species- and lake-specific strategy was

beneficial in two regards: 1) it helped maintain consistency between the initial search and

the follow-up search, as species- and lake-specific keywords were common in the initial

search, and 2) it helped increase efficiency of the follow-up search process, which was

important because significant amounts of time had already been spent reviewing studies

during the initial search. Efficiency was further enhanced by filtering follow-up searches

using the "Fisheries" and "Marine and freshwater biology" search areas as well as the

"article" document type in the Web of Science interface. Follow-up searches also only

targeted studies published from 1980 onward. 1980 was chosen as the cut-off year

because none of the six studies used in the current research (that were found during the

initial search) were published prior to 1984. Further, to ensure follow-up searches used

keywords well-suited to the goals of the initial search, care was taken to use keywords

common to two or more of the six studies.

      Consistent with attempts made during the initial search, the first part of the

follow-up search was specifically targeted at Yellow Perch due to reasons provided in the

Introduction section of the current research (i.e. they are native and considered innocuous

in many areas of Canada, but considered invasive in southern BC), and the second part of

the follow-up search was specifically targeted at carp because of the significant

popularity of this group in North America. Also consistent with attempts made during

the initial search, the third part of the follow-up search was specifically targeted at Lake

Michigan. Lake Michigan was chosen because it is a great study site for examination of

interactions between invasive and native fish species due to its long history of invasions

(Smith and Tibbles 1980; Mills et al. 1993).

The follow-up search consisted of two rounds of rejections. In the first round, rejection of initial results found was based on at least one of three reasons, the first two reasons being common to all three parts of the follow-up search and the third reason differing between parts. The first reason for rejection was no indication within the titles of the studies that the corresponding research examined trophic interactions and/or overlap between at least one native and at least one invasive fish species. The second reason for rejection was indication within the titles of the studies that the corresponding research was not based on an invasion that had occurred independent of the research (i.e. fish were stocked for the purpose of the study). The third reasons for rejection in the first, second, and third parts, respectively, of the follow-up search were 1) titles indicated main species studied were not Yellow Perch, 2) titles indicated main species studied were species not belonging to the carp group, and 3) titles indicated studies were targeted at areas other than Lake Michigan.

After the first round of rejections, the body of each remaining study was searched for evidence of substantial trophic overlap between native and invasive fish species and either 1) enough information to estimate FCR, RMR and GR, or 2) some form of evaluation of bioenergetic rates in both species groups. Failure to meet these conditions resulted in rejection. As well, similar to the first round of rejections, studies were rejected if it was discovered that invasions had not occurred independent of the research.

In the end, the number of results not rejected was determined for each part of the follow-up search (i.e. Yellow Perch, carp, and Lake Michigan) and divided by the number of initial results found in each part as well as the number of studies having not been rejected in rejection round one of each part, thus providing two groups containing

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measures of success for each of the three parts. The arithmetic means of each group were calculated to provide two overall measures of success (one based on the number of initial results found, and one based on the number of studies remaining after the first round of rejections).

RESULTS

Case-histories of Invasive Fishes

Bighead and Silver Carp in La Grange Reach, Illinois River.—Irons *et al.* (2007) studied body condition of Gizzard Shad *Dorosoma cepedianum* and Bigmouth Buffalo *Ictiobus cyprinellus* prior to and after introductions of Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *H. molitrix* in La Grange Reach, Illinois River. Bighead Carp were first observed in La Grange Reach in 1995, and Silver Carp in 1998. Peak catch of Bighead Carp occurred in 2000, and Silver Carp in 2004. Body condition of Gizzard Shad and Bigmouth Buffalo were both shown to have declined as commercial harvest of the two carp species increased, suggesting relationships between Gizzard Shad and Bigmouth Buffalo body condition and carp abundance. Nineteen abiotic and biotic factors were tested for relationships with body condition of Gizzard Shad and Bigmouth Buffalo, but no trends were observed with any of the factors except year, providing strong indication declines in body condition were a result of effects of carp. The researchers did not provide weight or length information for fish caught, but Sampson *et al.* (2009) collected all four species from the Illinois and Mississippi Rivers between late May and mid-June 2002 and 2003 for their analysis of diet overlap. Sampson *et al.* (2009) indicated all four species occupied the same habitat at this time. They found most

diet overlap between Silver Carp, Bighead Carp, and Gizzard Shad. The current research

used only these three species for bioenergetic comparisons, with zooplankton as prey,

since zooplankton was found to be a common prey item for Silver Carp, Bighead Carp,

and Gizzard Shad (Sampson *et al.* 2009). Energy density of zooplankton was 1987 J • g^{-1}

(Cummins and Wuychuck 1971; Lantry and Stewart 1993). Energy density of Gizzard

Shad was 5233 J • g^{-1} (Stewart and Binkowski 1986; Sebring 2002), while Bighead and

Silver Carp energy density was 5442 J • g^{-1} (Cooke and Hill 2010). Water temperature

was set at 26.67°C, since this is the average of the FTPs for the three species analyzed

(25°C for Gizzard Shad (Sebring 2002), 26°C for Bighead Carp, and 29°C for Silver

Carp (Cooke and Hill 2010)), and since habitat overlap was indicated by Sampson *et al.*

(2009). Total length of Gizzard Shad ranged from 82-427mm, Bighead Carp from 439-

1002mm, and Silver Carp from 261-798mm (Sampson *et al.* 2009). Median length

values were used for each species, with length converted to weight using collections of

length-weight regressions found on FishBase (FishBase 2015). Resulting weights were

242-, 5545-, and 2483g for Gizzard Shad, Bighead Carp, and Siler Carp, respectively.

Activity multipliers for Bighead and Silver Carp were set to 1.7, which is conservative

based on the suggestion of 2 by Winberg (1956). Table 2.1 lists weight, temperature,

prey energy density, and predator energy density of the three species analyzed.

Table 2.1. Inputs used in bioenergetic calculations comparing food consumption rates, routine metabolic rates, and growth rates of Gizzard Shad *Dorosoma cepedianum*, Bighead Carp *Hypophthalmichthys nobilis*, and Silver Carp *Hypophthalmichthys molitrix*.

	Gizzard Shad	Bighead Carp	Silver Carp
Weight (g)	242	5545	2483
Temperature (°C)	26.67	26.67	26.67
Prey energy density (J • g^{-1})	1987	1987	1987
Predator energy density (J • g^{-1})	5233	5442	5442

*Lake Trout in Hector Lake, Alberta.—*Donald and Alger (1993) studied

displacement of Bull Trout *Salvelinus confluentus* by introduced Lake Trout *Salvelinus*

namaycush in various mountain lakes in the Montana-Alberta-British Columbia area. Of

their analyses, the most comprehensive reporting was done for Hector Lake. They report

Lake Trout migrated to this lake after stocking had occurred 15km upstream, in Bow

Lake, Alberta, between 1964 and 1967. Complete replacement of Bull Trout in Hector

Lake occurred by 1984. The midsummer temperature for Hector Lake (8.2°C; Donald

and Alger 1993) was used for bioenergetic calculations. Donald and Alger (1993)

reported stomach content data for Bull Trout and Lake Trout ranging in weight from 16-

250g. The median value (133g) was used for calculations for both species. Donald and

Alger (1993) reported slight variations in diets between Bull Trout and Lake Trout (Table

2.2). From calculations based on diet information provided by Donald and Alger (1993)

as well as prey energy densities retrieved from literature, Bull Trout prey energy density

was set to 3492 J • g^{-1}, while Lake Trout prey energy density was set to 3668 J • g^{-1}.

Energy density for a 133g Bull Trout is 6189 J • g^{-1} (Mesa *et al.* 2013), and for a 133g

Lake Trout is 6111 J • g^{-1} (Stewart *et al.* 1983). The activity multiplier of a 133g Lake

Trout at 8.2°C is ~1.6 (Stewart *et al.* 1983), so activity of Bull Trout was set to the same

value. Table 2.3 lists weight, temperature, prey energy density, and predator energy

density of the two species analyzed.

Table 2.2. Diet information for Bull Trout *Salvelinus confluentus* and Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta, provided by Donald and Alger (1993). Energy densities were retrieved from literature.

	Energy density (J • g^{-1} wet mass)	Source	*% mass		Energy contribution to diet	
			Bull Trout	Lake Trout	Bull Trout	Lake Trout
Amphipoda	4429	Cummins and Wuychuck 1971	38	42	1683	1860
**Aerial insects	4526	Ciancio *et al.* 2007	25	3	1132	136
Cladocera	867	Cummins and Wuychuck 1971	20	11	173	95
Chironomidae	2922	Ciancio *et al.* 2007	16	16	468	468
Ephemeroptera	3675	Cummins and Wuychuck 1971	1	12	37	441
Dytiscidae	7616	Ciancio *et al.* 2007	-	5	-	381
Hirudinea	1243	Ciancio *et al.* 2007	-	6	-	75
Mountain whitefish *Prosopium williamsoni*	4246	Rudstam *et al.* 1994 (value for 5g generalized coregonid)	-	5	-	212
				Total:	3492	3668

*Donald and Alger (1993) provide % volume, but assumed 1 g • mL^{-1}
**value for Anisoptera

Table 2.3. Inputs used in bioenergetic calculations comparing food consumption rates, routine metabolic rates, and growth rates of Bull Trout *Salvelinus confluentus* and Lake Trout *Salvelinus*.

	Bull Trout	Lake Trout
Weight (g)	133	133
Temperature (°C)	8.2	8.2
Prey energy density (J • g^{-1})	5648	5648
Predator energy density (J • g^{-1})	6189	6111

Alewife in Southeastern Lake Michigan.—Crowder (1984) analyzed gill raker

number, fish habitat, and diet in Bloater *Coregonus hoyi* in southeastern Lake Michigan.

Crowder (1984) found a reduction in the number of gill rakers in Bloater following

Alewife *Alosa psuedoharengus* proliferation in the lake, which suggests a change in diet.

Prior to Alewife proliferation, Bloater < 150mm were not common in bottom trawls

(Wells and Beeton 1963; Crowder 1984), suggesting a pelagic distribution, whereas

Bloater were caught more frequently in benthic habitats after Alewife became abundant

(Crowder 1984; Crowder and Crawford 1984). Crowder and Crawford (1984) found

Bloater switched from pelagic zooplankton diets to benthic diets about 2 years earlier in

their lives than they did prior to the proliferation of Alewife. Crowder (1984) discussed

two reasons why an earlier diet shift was happening: 1) greater abundance of benthic prey

due to release from other sources of predation resulting from decreased abundance of

other deepwater ciscoes, and 2) greater predation on Bloaters due to more predators in the

lake as a result of stocking of Lake Trout, Coho Salmon, and Chinook Salmon.

However, Crowder (1984) suggested the first hypothesis was unlikely because there is a

lack of documented evidence of a shift in the diet of young Bloaters corresponding to the

decline of deepwater ciscoes in the lake. It seemed young Bloaters had not shifted their

diet until well after the decline of deepwater ciscoes. Crowder (1984) also suggested the

second hypothesis was unlikely because the predators introduced to the lake are not

known to eat Bloaters. As such, the study of Crowder (1984) concluded the earlier diet

shift in Bloaters was likely due to competition with Alewife. The upper size reported by

Crawford (1984; 135mm standard length) was used in bioenergetic calculations of the

current research. This length equated to a weight of 48g using collections of length-weight regressions found on FishBase (FishBase 2015). Alewife size was assumed to be the same as Bloater (48g). Crowder (1984) stated pelagic Bloaters consume mostly zooplankton. Since the current research is interested in the competitive effects that caused the diet shift mentioned previously, zooplankton was assumed to be the main dietary item for both Bloaters and Alewife, with a prey energy density of 1987 $J•g^{-1}$ (Sebring 2002). Water temperature was set to 16.85, which is the average FTP of Bloater (16.8) and Alewife (16.9). Energy density for a 48g Bloater is 6770 $J • g^{-1}$ (Rudstam *et al.* 1994), and Alewife energy density of 5233 $J•g^{-1}$ was provided by Stewart and Binkowski (1986). Table 2.4 lists weight, temperature, prey energy density, and predator energy density of the two species analyzed.

Table 2.4. Inputs used in bioenergetic calculations comparing food consumption rates, routine metabolic rates, and growth rates of Bloater *Coregonus hoyi* and Alewife *Alosa psuedoharengus*.

	Bloater	Alewife
Weight (g)	48	48
Temperature (°C)	16.85	16.85
Prey energy density ($J • g^{-1}$)	1987	1987
Predator energy density ($J • g^{-1}$)	6770	5233

Figures 2.1 to 2.3 display bioenergetic rates of species analyzed in the current research: Figure 2.1 is FCR, Figure 2.2 is RMR, and Figure 2.3 is GR. For each case-history analysis, percent differences were calculated between FCR, RMR, and GR of invasive and native fish. These bioenergetic ratios of native:invasive species are provided in Table 2.5. For each case-history, the FCR, RMR, and GR was higher for the

invasive species compared to the native species with the exceptions of Gizzard Shad versus Bighead Carp for FCR and RMR, Gizzard Shad versus Silver Carp for GR, and Bull Trout versus Lake Trout for GR. The greatest difference in bioenergetic rates was for RMR between Gizzard Shad and Bighead Carp (ratio = 2.04). The smallest difference in bioenergetic rates was for GR between the same two species (ratio = 0.99).
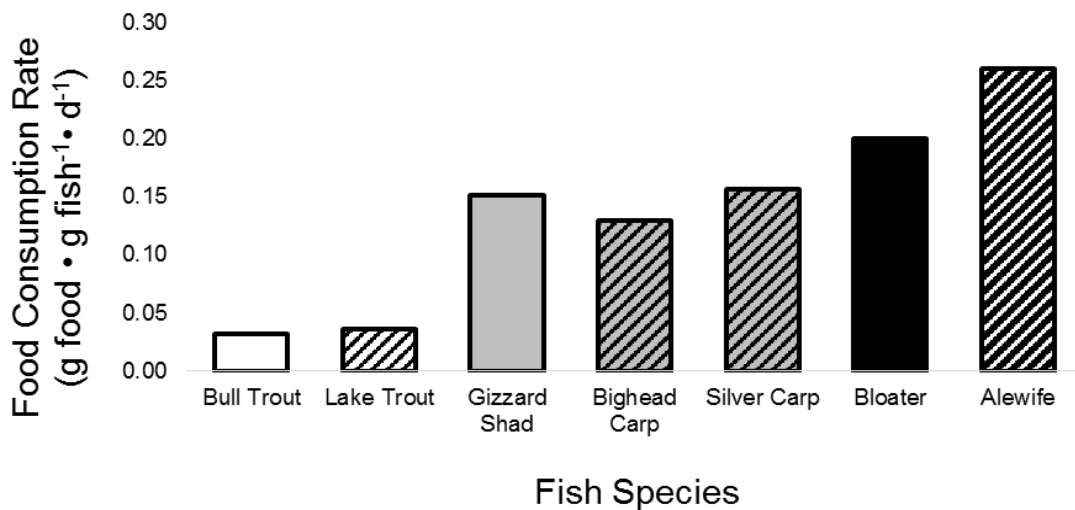
Figure 2.1. Food consumption rates of native Bull Trout *Salvelinus confluentus* and invasive Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta (white bars); native Gizzard Shad *Dorosoma cepedianum* and invasive Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix* in La Grange Reach, Illinois River (gray bars); and native Bloater *Coregonus hoyi* and invasive Alewife *Alosa pseudoharengus* in Lake Michigan (black bars). Solid bars indicate native species and striped bars indicate invasive species.
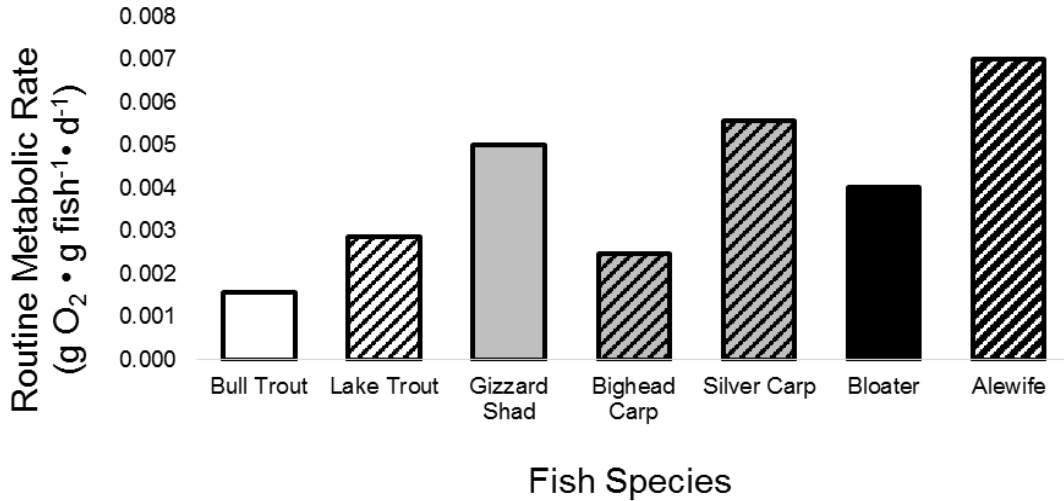
Figure 2.2. Routine metabolic rates of native Bull Trout *Salvelinus confluentus* and invasive Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta (white bars); native Gizzard Shad *Dorosoma cepedianum* and invasive Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix* in La Grange Reach, Illinois River (gray bars); and native Bloater *Coregonus hoyi* and invasive Alewife *Alosa pseudoharengus* in Lake Michigan (black bars). Solid bars indicate native species and striped bars indicate invasive species.
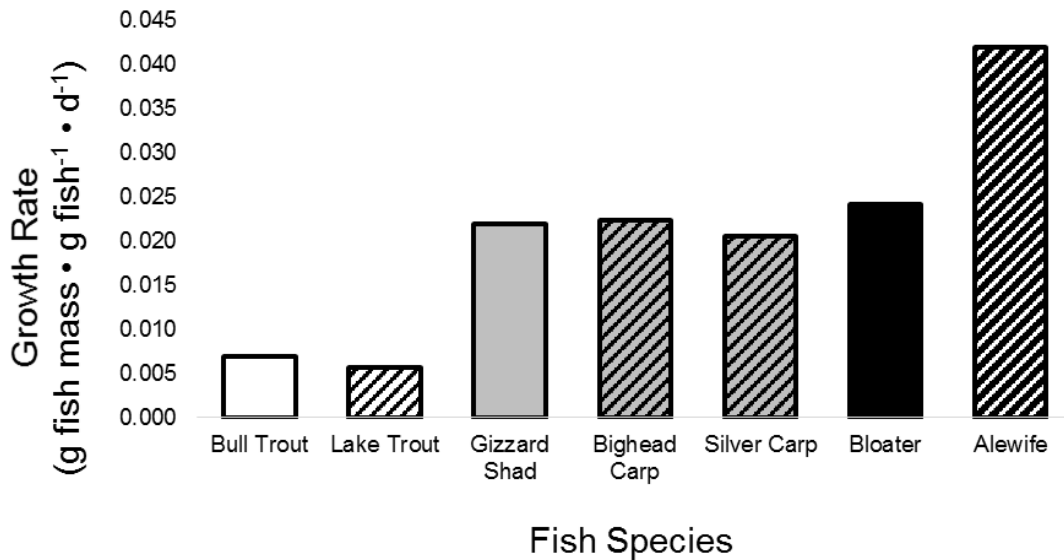
Figure 2.3. Growth rates of native Bull Trout *Salvelinus confluentus* and invasive Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta (white bars); native Gizzard Shad *Dorosoma cepedianum* and invasive Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix* in La Grange Reach, Illinois River (gray bars); and native Bloater *Coregonus hoyi* and invasive Alewife *Alosa pseudoharengus* in Lake Michigan (black bars). Solid bars indicate native species and striped bars indicate invasive species.

Table 2.5. Ratios of food consumption, routine metabolic, and growth rates for co-existing native and invasive species. Species compared are native Bull Trout *Salvelinus confluentus* and invasive Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta; native Gizzard Shad *Dorosoma cepedianum* and invasive Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix* in La Grange Reach, Illinois River; and native Bloater *Coregonus hoyi* and invasive Alewife *Alosa pseudoharengus* in Lake Michigan.

Comparison (native vs. invader)	Food consumption rate (g food • g fish^{-1} • day^{-1})	Routine metabolic rate (g O$_2$ • g fish-1 • day-1)	Growth rate (g fish mass • g fish^{-1} • day^{-1})
Bull Trout vs. Lake Trout	0.90	0.54	1.20
Gizzard Shad vs. Bighead Carp	1.17	2.04	0.99
Gizzard Shad vs. Silver Carp	0.97	0.90	1.07
Bloater vs. Alewife	0.77	0.57	0.58

Case-studies of Invasive Fishes

Rainbow Smelt in Crystal Lake, Wisconsin.—Rainbow Smelt were found in Crystal Lake in 1985 and had displaced Yellow Perch as the dominant fish in the lake by 1994 (Hrabik *et al.* 1998). Hrabik *et al.* (1998) found evidence of both thermal and diet overlap between Rainbow Smelt and Yellow Perch, as well as decreased relative condition in Yellow Perch with increasing Rainbow Smelt abundance. However, despite low abundance of Yellow Perch, these fish were still found to be recruiting, and juvenile Yellow Perch were largely unaffected by Rainbow Smelt due to differences in thermal preference. Thus, competition between the two species, as opposed to predation of Rainbow Smelt on Yellow Perch, was considered to be the mechanism behind the declines in Yellow Perch abundance and relative condition. Taking the Crystal Lake analysis one step further, Hrabik *et al.* (2001) analyzed age-0 life stages of Rainbow Smelt and Yellow Perch. Numerous reasons were cited as to why age-0 fish provide a

good life stage to study trophic interactions, including opportunity to study trophic overlap in species that do not occupy similar habitats at later life stages, since fish generally prefer warmer water at young ages. In this case, age-0 Rainbow Smelt and Yellow Perch were found to occupy similar locations in spring and summer and displayed significant diet overlap. Hrabik *et al.* (2001) compared the proportion of maximum food consumption being met in Yellow Perch from the 1981-1994 pre-invasion period to the post-invasion period in 1995-1996 and found significantly lower values post-invasion ($\geq 45\%$ vs. $\leq 30\%$). *Diaptomus* was an important prey for both Rainbow Smelt and Yellow Perch, but declined as FCR of Rainbow Smelt increased. Proportion of maximum food consumption in Yellow Perch was shown to correlate with *Diaptomus* abundance. These observations suggested increased feeding on *Diaptomus* by Rainbow Smelt led to decreased abundance of this prey, resulting in reduced food availability, and therefore reduced feeding rate, for Yellow Perch.

Chinook Salmon in Lake Michigan.—Smith (1968) provided an early account of salmonid stocking in Lake Michigan. In summary, parasitism by invasive Sea Lamprey had contributed to declines in Lake Trout abundance. Without many large, predatory fish in the lake, invasive Alewives were able to flourish. Lake Trout stocking began in 1965 to reestablish the population. To help control Alewife populations, a variety of non-native salmon were also introduced, including Chinook and Coho Salmon and Steelhead Trout. Smith (1968) reported Coho Salmon feeding on Alewives in the mid- to upper portion of the lake, and predicted Chinook and Steelhead would utilize the same area once they became established. However, Smith noted it was unlikely all introduced predators would reach high abundances in the system, and he expressed concerns about

the lake having only one species of forage fish available at the time (Alewife). On average across all the Great Lakes, more Chinook Salmon were stocked than any other salmonid from 1983-1993, as they were shown to be a productive species due to their rapid rate of maturity, as well as a desirable species to anglers due to their large adult size (Kocik and Jones 1999). Harvest from Lake Michigan from the early 1970s to late 1990s was mostly Chinook, followed by Coho, and then other salmonids (Holey *et al.* 1998).

Results of modeling by Stewart and Ibarra (1991) for salmonids in Lake Michigan showed dominance in total food consumption by Chinook Salmon over both Coho Salmon and Lake Trout. Chinook and Coho Salmon also both had higher gross conversion efficiencies than Lake Trout from 1978-1988 (Stewart and Ibarra 1991), meaning they were more efficient at turning the lake's resources into their own body mass compared to Lake Trout. From these observations, it is evident Chinook Salmon had greater abilities to restructure the Lake Michigan ecosystem than Lake Trout.

*White Perch in Lake Erie.—*White Perch *Morone americana* were first observed in Lake Erie in 1953 (Larsen 1954). Parrish and Margraf (1990) hypothesized competitive interactions between White Perch and Yellow Perch in the lake. These researchers built upon previous work by Hayward and Margraf (1987) that looked at the effects of eutrophication on Yellow Perch in the western and central basins, noting the rate of decline in growth of Yellow Perch increased after White Perch invaded. Parrish and Margraf (1990) compared FCRs, diets, and growth between White Perch and Yellow Perch from the western and central basins between May and November, 1983-1985. Diet overlap was based on both size and taxonomy of prey using the Schoener (1970) index. In general, they found FCRs of both White and Yellow Perch were higher in the central

40

basin than the western basin. They also reported higher FCRs (by as much as 27%) for

White Perch compared to Yellow Perch. Significant diet overlap was found in 52%

(25/48) of comparisons. The authors noted the FCRs measured for White Perch (up to

0.219 g food • g fish^{-1} • d^{-1}) were among the highest values found when compared to

other fish species. For Yellow Perch, FCR was comparable to other north-temperate

lakes (i.e. Lake Memphremagog, Quebec-Vermont (Nakashima and Leggett 1978)).

Figures presented in Parrish and Margraf (1990) showed higher growth rate in White

Perch than Yellow Perch in Lake Erie, yet they found no difference in growth of White

Perch between basins despite greater FCR in the central basin than the western basin.

Hayward and Margraf (1987) found differences in growth rate of Yellow Perch between

basins, with reduced growth rate in the western basin (more eutrophic), which they

attributed to lower FCR. Parrish and Margraf (1990) suggested White Perch growth rate

may have been similar between basins due to a temperature effect, as their higher thermal

preference compared to Yellow Perch would allow higher growth rates with lower FCR

in the warmer waters of the western basin compared to the central basin. As well, Parrish

and Margraf (1990) suggested little was known about White Perch migrations in Lake

Erie at the time of their study, so possible mixing of fish between the western and central

basins could have occurred at some point.

Follow-up Literature Search

Keywords (i.e. "topics") for the first, second, and third parts of the follow-up

search were: "Yellow Perch" and "interactions" for the first part, "carp" and

"competition" for the second part, and "Lake Michigan" and "competition" for the third

part. "Interactions" was chosen as a keyword in the Yellow Perch-specific part of the follow-up search because it was common to titles of two of six studies (Parrish and Margraf 1990; Hrabik *et al.* 2001) used in the current research (that were found during the initial search), both of which involved Yellow Perch. "Competition" was chosen as a keyword in the carp- and Lake Michigan-specific parts of the follow-up search because it was common to titles of two of six studies (Crowder 1984; Irons *et al.* 2007) used in the current research, one of which (Irons *et al.* 2007) involved carp, and the other of which (Crowder 1984) involved Lake Michigan.

The first, second, and third parts of the follow-up search yielded 125 (124 of which had free access), 102 (101 of which had free access), and 101 results (Yellow Perch, carp, and Lake Michigan parts, respectively). Of the free-access studies, 107, 90, and 93 were rejected in the first round of rejections. Of the 17, 11, and 8 remaining studies, 12, 10, and 8 were rejected in the second round of rejections, leaving 5, 1, and 0 studies that were not rejected at all. The success rates based on the numbers of studies not rejected (after both rounds of rejections) divided by the numbers of initial studies found for the first, second, and third parts of the follow-up search were 4.0%, 1.0%, and 0.0%, with a mean value of 1.7%. The success rates based on the numbers of studies not rejected (after both rounds of rejections) divided by the numbers of studies remaining after the first round of rejections were 29.4%, 9.1%, and 0.0%, with a mean value of 12.8%. To summarize, passing criteria were met for 1.7% of initial results and 12.8% of studies having titles suggesting research applicable to the current work. Main reasons for second-round rejections are summarized in Table 2.6.

Table 2.6. Number of, and reasons for, rejections of studies obtained through a literature search using Web of Science with the purpose of quantifying effort required to find studies adequately allowing assessment of trophic impact of invasive relative to co-existing native fish species through two objectives: 1) provide and compare measures of FCR, RMR, and GR of invasive and co-existing native fish species based on actual scenarios, and 2) summarize actual scenarios that evaluated one or more of FCR, RMR, and/or GR in invasive compared to co-existing native fish species. Note: some studies were rejected for multiple reasons.

Reason for rejection	Number of studies rejected
study done in laboratory, or species stocked for purpose of study	6
no mention of trophic overlap, or trophic overlap found to be insignificant	5
insufficient data to calculate bioenergetic rates of co-existing invasive and native fish species	8
insufficient evaluation of bioenergetic rates of co-existing invasive and native fish species	8
not a study of a native versus invasive fish species	6
focus does not include competition for food (e.g. predation, shared habitat)	4
at the time the study was written, the non-native fish species had not yet proven to be invasive in the study area	1

DISCUSSION

With four exceptions, the current research has demonstrated invasive fish species often have higher FCR, RMR, and GR than native species when food resources are shared. The exceptions were GR in Bull Trout and Lake Trout (20% greater for Bull Trout), FCR and RMR in Gizzard Shad and Bighead Carp (17% and 104% greater, respectively, for Gizzard Shad), and GR of Gizzard Shad and Silver Carp (7% greater for Gizzard Shad). The greater energetic demands (RMR and GR) of invasive species relative to native species necessitate a need for invasive species to consume greater

quantities of food, thus having a greater trophic impact on ecosystems than native species. Further, the heightened GRs of invasive over native species result in greater mass-at-age, or attainment of a larger size in less time, which may make invasive species more dominating in competition for food in some situations. Among the findings of the case-studies analyzed here, it has been shown that native species often respond to competition from invasive species through reduced FCR, GR, or body condition (Parrish and Margraf 1990; Hrabik *et al.* 2001), or by switching to different sources of prey (Crowder 1984). Reduced GR of species in the commercial fishery is of importance because smaller fish mean reduced payoff per unit of time spent fishing. As well, reduced GR may translate into delayed maturity (Rowe and Thorpe 1990), thereby prolonging the period of pre-maturation mortality and resulting in fewer spawning individuals. Further, slowed growth may mean reduced reproductive output for a species, since reproductive output increases with fish weight (Blueweiss *et al.* 1978). Reduced growth of important recreational species is detrimental to sport fishing, including the tourism industries built around this activity. When the impact of an invasive species includes a shift in diet of the native species, negative consequences can include reduced growth from consuming nutritionally poorer quality prey as well as increased pressure on the new prey source, which may result in competition between the displaced species and other species already feeding on that prey source.

The comparison involving Gizzard Shad, Bighead Carp, and Silver Carp was unique in the current research in that the native species (Gizzard Shad) did not consistently demonstrate lower bioenergetic rates than the invasive species (Bighead Carp and Silver Carp). For this analysis, bioenergetic rates were calculated using weights

derived from median lengths reported for each of the three species. The weight used for

Gizzard Shad (242g) was more than 10 times lower than that of either Silver (2,483g) or

Bighead (5,545g) Carp. Since bioenergetic rates are influenced by allometry (Kleiber

1932; Peters 1983; Hanson *et al.* 1997), larger Gizzard Shad would have lower FCR,

RMR, and GR, perhaps even lower than those of the invasive species examined, as was

expected.

The comparison between Bull Trout and Lake Trout in Hector Lake demonstrated

much lower bioenergetic rates than the other comparisons made, which should come as

no surprise. Hector Lake, Alberta, experiences an average midsummer water temperature

of 8.2°C and sits at 1752m above sea level (Donald and Alger 1993). Alpine lakes are

typically of much lower productivity owing to low inputs of external nutrients and lower

water temperatures (Sommaruga *et al.* 1999), resulting in fewer food resources for fish.

The delicate nature of cold water ecosystems makes them susceptible to change, leaving

no room for introduction of invasive species when change may be detrimental. Donald

and Alger (1993) commented on the effects of varying trophic structures among the lakes

analyzed including stunting of Bull Trout and Lake Trout in lakes lacking amphipods and

fish. In Hector Lake, both trout species relied to a great extent on amphipods, but Bull

Trout did not consume fish, while Lake Trout consumed ~5% Mountain Whitefish

Prosopium williamsoni. As such, one would expect moderately stunted growth in this

lake for both species of trout. The authors report similar growth for both Bull Trout and

Lake Trout in Hector Lake, although the bioenergetic comparisons of the current research

demonstrated a ratio of 1.2 for Bull Trout GR : Lake Trout GR. Since these two species

had slightly different diets in Hector Lake (Donald and Alger 1993), differences between

prey energy densities retrieved from literature and those actually occurring in the Hector

Lake area may explain the variation between GR results of Donald and Alger (1993) and

the current research. It is common for energy densities within species to vary from one

location to another. For instance, Pothoven *et al.* (2006) reported a difference of up to

23% in energy density of Lake Whitefish *Coregonus clupeaformis* from Lake Michigan

versus Lake Huron.

Lake Trout are of particular interest in the current research because they were the

invasive species in Hector Lake, but the native species in Lake Michigan. Compared to

Bull Trout in Hector Lake, Lake Trout demonstrated higher FCR and RMR. However, in

Lake Michigan, Chinook Salmon showed greater FCR at the population level and greater

conversion efficiency than Lake Trout (Stewart and Ibarra 1991). Hence, it is important

to analyze native species relative to AIS on a habitat-specific bases prior to making

management decisions.

A drawback of the current research was failure to take into account durations in

which species examined were not displaying trophic overlap. For instance, the research

by Sampson *et al.* (2009) studying native and invasive fishes in the Illinois and

Mississippi Rivers used samples collected in late May to mid-June because this was when

most habitat overlap occurred between species. Indeed their results indicated high diet

overlap between Gizzard Shad and the carp species, but if this overlap occurred only part

of each year, there is question as to whether it alone is the reason behind the reduced

body condition in Gizzard Shad observed by Irons *et al.* (2007) in La Grange Reach,

Illinois River, or if other factors were at work. For this reason, it would be beneficial to

analyze habitat and diet overlap throughout the year, or at least throughout the growing

season. However, in the case of Gizzard Shad and carp species in the Illinois River, Irons *et al.* (2007) did not find any correlations between body condition in Gizzard Shad and any of the possible causal abiotic and biotic factors analyzed except commercial carp harvest (which may reflect abundance) and year. Spring represents a critical time for many organisms, as warming temperatures and increased food supply from growth of primary producers and recruitment of new individuals make for good growing conditions if species can take advantage. As such, even short periods of habitat and diet overlap between species could have negative effects on growth.

Although the current research provides evidence of a link between bioenergetic rates and impact, research has demonstrated impact may occur from introduced fish species not having greater bioenergetic rates than native species. For instance, Schulze *et al.* (2006) studied effects of introduced Zander *Sander lucioperca* on native Northern Pike and Eurasian Perch *Perca fluviatilis* in Lake Grober Vatersee, Germany. They stocked Zander in the lake in 2001 and 2002. As a result of introduced Zander, FCR of Northern Pike increased while FCR of Eurasian Perch decreased. The authors observed a habitat shift in prey fish toward the littoral zone and suggested the increased availability of food in this area may have been responsible for the increased FCR of Northern Pike, which were also found to inhabit the littoral zone. The authors also suggested there was competition between Eurasian Perch and Zander. Thus, even though Zander had the lowest FCR of the three species analyzed, they still had trophic impact by directly competing with, and reducing FCR of, Eurasian Perch.

In many situations, the impacts of AIS are dependent on prior anthropogenic changes in recipient environments. Previous local adaptations of native species may not

be beneficial in altered environments, and some AIS may actually be better adapted to the anthropogenic changes (Olden *et al.* 2006). Angermeier (1995) studied extirpated fish species in Virginia and found multiple anthropogenic stressors were a contributor of extirpations, and the case-study used in the current research of Yellow Perch and White Perch in Lake Erie provides a good example of how anthropogenic change can be detrimental to a native species but beneficial to an AIS. In this case, eutrophication of Lake Erie had already led to declined feeding and growth of Yellow Perch through reduced prey size (Hayward and Margraf 1987). It was hypothesized White Perch may have not been as negatively affected as Yellow Perch by eutrophication in Lake Erie due to higher thermal preference than Yellow Perch (Parrish and Margraf 1990).

The current research has shown invasive species often have higher bioenergetic rates than native species when the two co-exist. However, it was demonstrated that finding studies providing sufficient information to conduct the research presented here was difficult. Among the reasons for studies not being adequate in terms of the criteria mentioned previously, insufficient data to calculate bioenergetic rates of co-existing invasive and native fish species, as well as insufficient evaluation of bioenergetic rates of co-existing invasive and native fish species were the two most regularly encountered. As such, it is suggested researchers examining interactions and/or competition between invasive and native fish species either provide all information needed to calculate bioenergetic rates for both species, or provide some evaluation of bioenergetic rates for both species (FCR, RMR, or GR). In addition, due to environmental differences and differences in resident native fish from one location to the next, there is a need to consider AIS trophic impact on a case-by-case basis, and to especially consider

influences of previous anthropogenic changes in recipient environments on native and introduced species. As well, to gain a better understanding of the importance of short periods of competition in determining magnitude of trophic impact, there is a need to monitor interactions between species over an entire growing season to assess relationships between timing, duration, and frequency of habitat and diet overlap and trophic impacts realized. The most devastating effects may be realized during critical times of year, such as times of heavy feeding or spawning. Lastly, it is important to understand AIS with lower bioenergetic rates than native species may still produce ecosystem changes.

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CHAPTER 3

EXPLORING RELATIONSHIPS BETWEEN FISH TRAITS AND ROUTINE

METABOLIC RATES: A POTENTIAL TOOL TO ASSESS AQUATIC INVASIVE

SPECIES TROPHIC IMPACT

INTRODUCTION

Numerous inland water systems, a large coastal area, and frequent vehicular traffic make much of North America susceptible to the invasion and spread of aquatic invasive species (AIS; CCFAM Aquatic Invasive Species Task Group 2004). Invasive species cost the United States approximately $137 billion annually (Primentel *et al*. 2000; Colautti *et al.* 2006), and costs in Canada due to impacts of AIS total between $7.5 and $35 billion per year (Dawson 2002; Colautti *et al.* 2006). AIS can spread across land and overseas through numerous pathways (Kerr *et al.* 2005) including ballast water, canals, and intentional and unintentional release (Ludwig and Leitch 1996; Johnson *et al*. 2001; Naylor *et al.* 2001). Despite advancements in regulations associated with pathways, and reduction in AIS introduced via ballast water, AIS still continue to invade, with invasions through water gardens and the pet and aquarium trades becoming more important. The invasion rate of AIS in the Laurentian Great Lakes (hereafter referred to as the Great Lakes) over only the past 55 years is over 1.6 times the invasion rate for the preceding 175 years (Ricciardi 2006). It is not feasible to manage for all AIS coming in to North America (OTA 1993) due to the numerous pathways, frequent imports, high rates of invasion, and diversity of species coming in, but prevention strategies have been suggested (Clavero and Garcia-Berthou 2005), and prevention is by far the most

economically and effective method to reduce future invasion risk (Finnoff *et al.* 2007).

Knowing which invaders pose the greatest threat of impact prior to their invasion would

be beneficial in determining where to allocate preventative resources or management

immediately following arrival.

Of the many aquatic species, much attention has been directed toward invasive

fish due to the economic and recreational benefits of fishery resources. The Great Lakes

fishery alone is currently valued at $7 billion each year (American Sport Fishing

Association 2008; Dettmers *et al.* 2012), and AIS are seen as the second-leading threat to

biodiversity (Clavero and Garcia-Berthou 2005; Ricciardi 2007). Great efforts have been

put forth to manage AIS in the Great Lakes and other regions of North America, yet new

species continue to become established, contributing to reduced production of important

fisheries by disrupting energy flows and ecosystem processes, compromising water

quality, damaging infrastructure, preying and parasitizing other organisms, displacing and

hybridizing with native species, and introducing new diseases. The variety of impacts

AIS can have makes it complicated to predict which ones require management attention.

As such, it is necessary to analyze each type of impact individually. This research

focuses on trophic impact, which is defined here as resource depletion through feeding.

Bioenergetics models are used to study energy dynamics, including food

consumption rate (FCR) and energetic costs in fish. FCR can provide direct insight into

magnitude of trophic impact (Liao *et al.* 2005; Dick *et al.* 2012) since higher FCRs

hasten resource depletion, affecting other organisms. For instance, introduced fish

species may prey directly on native fish species or compete with native fish species for

food, causing shifts in the production and compositions of ecosystems (Vander Zanden *et*

al. 1999). Routine metabolic rate (RMR), which amalgamates standard (resting) metabolic rate (SMR) with costs of spontaneous activity (Beamish and Mookherjii 1964), is closely tied to FCR, as indicated by bioenergetics mass-balance principles (Winberg 1956). An estimated 37-44% of the energy budget of a fish is allocated to RMR (Brett and Groves 1979), indicating a strong link between FCR and RMR. In the absence of FCR data, RMR can serve as a surrogate. However, although RMR data are easily available for a number of fish species, data does not always exist for AIS of concern.

Obtaining data through respirometry trials is time, labour, and resource-intensive, requiring trained technicians and specialised equipment. Attention must be paid to controlling for various factors that may affect RMR (Steffensen 1989). For instance, elevated RMR readings can occur if fish are not fasted long enough, as respiration will increase due to effects of specific dynamic action. Measurements may be up to 10% different if fish are fasted 48 hours as opposed to only 24 hours (Brett 1962). Fish must also be acclimatized to temperature and oxygen levels in respirometry tanks, a process which may take up to 20 days (Brett 1962). As well, oxygen levels must be kept constant and equal for each species, as species with less capacity to extract oxygen from water will be less able to cope with low levels. When measurements are required for numerous species, controlling for the various factors makes respirometry a very time-consuming process. In such instances, generalized models to estimate RMR would prove useful.

Palomares and Pauly (1998) developed multiple regression models to predict consumption per unit biomass (Q/B) from analysis of fish traits. Since FCR and RMR are closely linked, the work of Palomares and Pauly (1998) suggests there may be relationships between RMR and fish traits that allow prediction of the former given data

on the later, providing the ability to predict which species of concern consume the most

energy and, thus, pose the greatest threat of trophic impact. Similar to multiple

regression models, classification trees (CTs) make use of many independent variables to

predict an outcome. An advantage of CTs over multiple regression models is they

require no mathematical calculations upon application and have a graphically user-

friendly output. A disadvantage to CTs is their structures can vary greatly after removing

or adding a few observations (Cutler 2010). Random forests (RFs) comprise a number of

unpruned (i.e. growth to their maximum) CTs made from random samples of the total

sample set (in this case, fish species), making RFs more robust to reduction or addition of

observations. CTs make no distributional assumptions, can handle missing values, and

do not require coding of categorical variables (Cutler 2010), and since RFs are composed

of many unpruned CTs, these freedoms carry over to RF analyses. In addition, RFs are

useful when there are many predictors but few observations, when independent variables

are of different types (continuous versus categorical), when categorical independent

variables are composed of different numbers of levels, and when correlations exist

between independent variables (Breiman 2001; Strobl *et al.* 2007; Strobl *et al.* 2009a;

Strobl *et al.* 2009b; Boulesteix *et al.* 2012). Further, RFs are not sensitive to outliers and

noise, and they do not overfit data (Breiman 2001), so there is no danger of increasing

error rate when using many trees in a RF. As well, RFs have proven more accurate

relative to other methods in an ecological context (Cutler *et al.* 2007) and are becoming

more popular in this field. Cutler *et al.* (2007) used RFs to predict presence of plant,

lichen, and bird species and compared prediction results to those obtained by linear

discriminant analysis, logistic regression, additive logistic regression, and CTs. Overall,

RFs outperformed all other methods, with prediction accuracies for RFs (percentage classified correctly) always > 80%, demonstrating the high predictive capability of RFs relative to other methods. The work of Cutler *et al.* (2007) included interacting variables as well as a wide range of sample sizes, including a RF involving only 23 samples, yet still accurate for 86% of predictions made. This level of accuracy demonstrates the ability of RFs to make accurate predictions despite low sample sizes. What is more, RFs can produce variable importance outputs, specifying how important independent variables are in predicting dependent variables. Cutler *et al.* (2007) emphasized how the results of variable importance procedures applied to habitat characteristics agreed with theoretical knowledge in describing location of certain plants.

Although RFs can be used for prediction, they do not provide easily interpretable outputs. In addition, to facilitate the best possible predictions, RFs have parameters requiring tuning. RFs can also be computationally expensive and take large amounts of time to generate, especially when generating variable importance scores. Nonetheless, by combining the strengths of RFs and CTs, robust and user-friendly models could be developed that are capable of predicting RMR, and thus, relative trophic impact, from analysis of easily-attainable fish traits.

The purpose of this research was to 1) examine variation in RMRs of freshwater (and highly anadromous), north-temperate ($\geq 40°$N latitude) fish species; 2) compile data on fish traits that may be descriptive of RMR; and 3) use RF and CT analyses to identify relationships between RMRs and fish traits to create models to predict relative trophic impact.

METHODS

Metabolic Rate Analysis

The amount of energy used by a fish for metabolism is dependent on fish size, water temperature, and activity. Weight- and temperature-dependent RMR parameters for 18 species of freshwater, north-temperate fish were obtained from Hanson *et al.* (1997), which contains physiologic parameter sets forming thebasis of bioenergetic models for a number of freshwater and marine fish and invertebrates. The bioenergetics equations conveniently allow estimation of RMR at any fish weight and water temperature. To increase sample size, physiologic parameter values for an additional 33 species of freshwater, north-temperate fish were retrieved from published literature and manuscripts in preparation. Finally, a search for additional RMR data (not necessarily summarized across weight and temperature) was conducted to facilitate representation of all major freshwater fish families in north-temperate freshwaters of North America. Care was taken to include representatives of families for species on current AIS fish watch lists. Collectively, the data set (n = 66 species) reflects the diversity of fish present and anticipated to establish populations in north-temperate freshwaters of North America. Owing to known weight- and temperature dependence, rates were compared at species-specific weight-at-maturity and final temperature preferendum (FTP; Beamish 1964).

It is common to borrow parameter values from similar species when constructing new metabolic or bioenergetics models. However, significant borrowing could have caused pseudo-replication in the current analysis. As such, in instances where nearly entire parameter sets were borrowed from similar species, only one of the species was

included. Further, in cases where data collected were taken at SMR as opposed to RMR, activity multipliers were used to scale SMR to RMR. Activity multipliers were estimated based on values for similar species owing to a lack of information describing energy allocated toward routine activity in various species.

Trait Analysis

Data for morphometric, physiologic, and ecologic traits expected to correlate with RMR (Table 3.1) were gathered from published literature and online sources. As mentioned previously, RFs are still useful when a dataset contains independent variables that are correlated (Strobl et al. 2009a), and although the inclusion of traits that may be highly correlated may seem redundant, correlation between two traits does not necessarily mean both traits will be equally valuable when used in a CT (i.e. one trait may simply result in groups of greater purity than the other trait). Further, when it came to choosing traits, some traits were chosen based not on expectations of correlations with RMR, but based simply on availability (for instance, eye diameter-to-head-length-ratio (ED)). As stated previously, RFs are not sensitive to noise (Breiman 2001) and they are useful in situations with many predictors relative to the number of observations (Strobl *et al.* 2009b). As such, adding variables not actually having relationships with RMR would not affect the statistical validity of the approach followed in the current research, as RF variable importance procedures would eliminate any variables unimportant in describing RMR, thereby preventing them from being incorportated into the CTs. Therefore, the addition of traits chosen based not on expectations of correlations with RMR was seen as an exploratory approach in the current research.

Brett and Groves (1979) found that carnivorous fish have higher metabolic costs than herbivores, so it was necessary to include trophic guild (TG) in the current analysis. In addition, caudal fin aspect ratio (CA) was included because it is correlated with food consumption (Palomares and Pauly 1998), as the shape of the caudal fin affects swimming speed (Sambilay 1990) and, therefore, energy use. Fish with a taller caudal fin relative to the size of the fin are more efficient swimmers (Sambilay 1990). Length has also been used as a predictor of swimming speed (Bainbridge 1958; Sambilay 1990). Hence, maximum total length (MTL) was included as an independent variable. Further, maximum weight (MW) was used because RMR decreases with increasing fish weight (Kleiber 1932; Kitchell *et al.* 1977).

Table 3.1. Independent variables analyzed for relationships with routine metabolic rate (RMR), showing representation from each of three trait classes (morphology, physiology, and ecology). Levels in categorical data were chosen based on levels used by source. Also shown are hypothesized relationships with RMR ("+" = positive relationship, "-" = negative relationship, NH = no hypothesis generated). See A6 for sources of data.

Trait class	Trait	Notation	Definition	Units	Number of levels	Reason for inclusion	Hypothesized relationship with RMR
morphology	maximum weight	MW	maximum weight recorded	g	-	Winberg 1956 (RMR decreases with fish weight); Palomares and Pauly 1998 (asymptotic weight has an effect on food consumption rate)	-
	maximum total length	MTL	maximum total length recorded	mm	-	Sambilay 1990 (body length is a predictor of swimming speed)	-
	standard length to total length ratio	SL	horizontal distance from tip of snout to end of caudal peduncle divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
	fork length to total length ratio	FL	horizontal distance from tip of snout to fork in tail divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
	pre-anal length to total length ratio	PA	horizontal distance from tip of snout to anal fins divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH

pre-dorsal length to total length ratio	PD	horizontal distance from tip of snout to proximal side of most proximal dorsal fin divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
pre-pelvic length to total length ratio	PPEL	horizontal distance from tip of snout to pelvic fins divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
pre-pectoral length to total length ratio	PPEC	horizontal distance from tip of snout to pectoral fins divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
body depth to total length ratio	BD	greatest vertical body depth divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	-
head length to total length ratio	HL	horizontal distance from tip of snout to distal end of gill plate divided by horizontal distance from tip of snout to most distal caudal fin tip	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	-
eye diameter to head length ratio	ED	eye diameter divided by horizontal distance from tip of snout to distal end of gill plate	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH
pre-orbital length to head length ratio	PO	horizontal distance from tip of snout to proximal side of eye divided by horizontal distance from tip of snout to distal end of gill plate	%	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	NH

				units			
	caudal aspect ratio	CA	height of caudal fin squared divided by surface area of caudal fin	-	-	Keast and Webb 1966 (body form is related to foraging activity); extension of Palomares and Pauly 1998 and Sambilay 1990 (lift and drag forces); easily available data	+
	body shape	BS	fusiform/normal, short/deep, elongate, eel-like	-	4	Keast and Webb 1966 (body form is related to foraging activity)	written in descending order of expected RMR in "Definitions" column
	mouth position	MP	terminal/superior, inferior	-	2	Keast and Webb 1966 (mouth position is related to foraging activity)	written in ascending order of expected RMR in "Definitions" column
physiology	K growth coefficient	K	von Bertalanffy growth coefficient	$cm \cdot year^{-1}$	-	Pearl 1928 (rate of living hypothesis)	+
	age at maturity	AM	average age at which maturity is reached	years	-	Fidhiany and Winckler 1998 (pattern in metabolism versus weight relationship is related to age)	-
	maximum lifespan	ML	maximum recorded lifespan	years	-	Pearl 1928 (rate of living hypothesis)	-
	maximum fecundity	MF	maximum recorded fecundity	eggs	-	easily available data	NH

ecology	trophic level	TRL	trophic position in food web	-	-	Brett and Groves 1979 (different energy allocations between carnivores and herbivores)	+
	trophic guild	TG	carnivore, omnivore, herbivore	-	3	Brett and Groves 1979 (different energy allocations between carnivores and herbivores)	written in descending order of expected RMR in "Definitions" column
	swim type	ST	carangiform/sub-carangiform, labriform/diodontiform, anguilliform	-	3	Korsmeyer *et al.* 2002 (differences in swimming efficiency depending on swim type)	written in descending order of expected RMR in "Definitions" column
	habitat preference	HP	benthopelagic/pelagic, demersal	-	2	Clark *et al.* 2013 (benthic fish have lower minimum and maximum oxygen consumption rates); Amundsen *et al.* 2004 (link between habitat choice and food type)	written in descending order of expected RMR in "Definitions" column

Korsmeyer *et al.* (2002) studied effects of different swimming types (STs) on oxygen consumption rate in parrotfish *Scarus schlegeli* and triggerfish *Rhinecanthus aculeatus* and found that, in these two species, a rigid-body ST using one or more median or paired fins for propulsion was more efficient than an undulating-body swim type using the caudal fin for propulsion. Korsmeyer *et al.* (2002) cite Webb (1998) as indicating the former ST is used more for enhancing maneuverability at low speeds, whereas the latter ST is more optimal at higher speeds, as it facilitates high propulsive force. Due to importance of ST in describing swimming efficiency, as well as the expectation active (i.e. high RMR) fish species should have traits enhancing swimming efficiency, ST was incorporated as a trait in the current analysis.

Clark *et al.* (2013) examined aerobic scope (the difference between minimum and maximum oxygen consumption rates) in pelagic and benthic fish species. Pelagic species have higher minimum and maximum oxygen consumption rates than benthic species and tend to focus more energy on maintaining swimming speed, while benthic species use more energy to digest food (higher SDA) and recover between ambush predatory events (Clark *et al.* 2013). In the current analysis, species analyzed were classified under habitat preference (HP) as either pelagic/benthopelagic or benthic. Pelagic and benthopelagic were grouped together because it is difficult to differentiate between the two.

Many traits related to physiology describe how quickly certain processes happen, such as growth and aging. In the case of rapid growth, rapidly occurring metabolic processes require increased energy supply. Pearl (1928) provided evidence that rate of energy expenditure over an organism's life is inversely related to lifespan (the "rate of living" theory), although in that case lifespan was the predicted variable and energy use

(RMR) was the predictor. Nonetheless, maximum lifespan (ML) was included as a predictor in the current analysis. In addition, Fidhiany and Winckler (1998) studied the effects of age on metabolism in the freshwater cichlid fish *Cichlasoma nigrofasciatum*. They found specific metabolic rate declines more rapidly prior to maturation than after. They suggested specific metabolic rate during rapid development is related to the amount of heat lost from the body due to increasing surface area. Smaller fish have a higher surface area to volume ratio, making the effects of external factors, such as temperature, greater on small fish than large fish. However, these researchers suggested after the adult stage is reached, metabolism is directed more toward maintenance and is less dependent on fish mass than it is on age. As such, both age at maturity (AM) and growth rate (K) are linked to metabolism and were therefore included in the current analysis.

Fish Datasets

Of the original dataset (n = 66 species), six (~9%) were removed using a stratified random approach and kept for model validation ("validation set") with the remaining 60 being used for model development ("main training set"). To enhance interpretability of final models, RMRs of fish in the main training set were divided into four categories based on quartiles (A, B, C, and D, listed in ascending order). This strategy worked well to ensure equal sample sizes in each category, although this is not a requirement of RFs. Four categories were chosen because three would result in reduced confidence when applying the model, as fish classified in the middle category (B) could be close to A or C, so when comparing two fish, confidence in results would only be obtained if one fish was classified as A and the other as C. Using more than four categories would result in

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increased model complexity with no apparent benefit. A disadvantage of using quartiles

was potentially forcing species of similar traits into different categories.

To observe if results remained consistent if species were removed, ten "reduced

sets" (n = 48 species each) were created by performing ten separate removals of three fish

from each quartile of the main training set, resulting in reduced sets having 80% of the

sample size of the main training set (Christina Semeniuk, personal communication, April

2015). Since data availability limited the number of independent variables included in

the main training set and reduced sets, a subset of fish ("subset", n = 49 species), for

which all data were found for all variables, was created from the original dataset to

examine importance of variables left out of the other analyses due to data limitations.

Similar to the main training set, the subset was subjected to categorization of RMRs

based on quartiles. However, no validation fish were removed from the subset.

Statistics

RFs (*party* package (Hothorn *et al.* 2006) in R) were used to determine which

variables were most important in classifying fish into categories for the main training set,

the reduced sets, and the subset. To differentiate between important and unimportant

variables, a threshold was established by taking the absolute value of the minimum

importance score, and values falling to the right of this threshold were deemed important

(Strobl *et al.* 2009b). Variable importance procedures were run twice, each time at a

different seed, to ensure enough trees were used in the RF to facilitate consistency of

results (Strobl *et al.* 2009a). From trials, it was determined an *ntree* (the total number of

trees in the RF) of 20,000 resulted in little inconsistency. As stated previously, there is

no danger in overfitting data when using many trees (Breiman 2001). For the main

training set and subset analyses, variables found important were analyzed again for

importance, after removal of unimportant variables, to ensure they remained important

when compared only to each other. A CT (*rpart* (Therneau *et al.* 2015) package in R,

plotted with *partykit* (Hothorn and Zeileis 2015) package in R) was created from the main

training set using only variables found important. As well, a second CT was created from

the main training set using only variables found consistently important in at least 7 of 10

reduced set variable importance procedures (the choice of 7 of 10 was not based on any

established rule). All fish from the validation set (n = 6 species) were put through both

CTs as a means of validation. Four passing predictions out of six were required for the

models to be considered successful (the choice of four out of six was not based on any

established rule).

For the RFs used in making predictions, dependent values were kept as

continuous data and variable importance procedures were rerun in the same way as for

categorized data. After variable importance procedures were applied to the uncategorized

RMRs, to ensure optimal predictive capability of prediction RFs, different values of *mtry*

(the number of independent variables randomly selected at each node in each tree, from

which one is selected for splitting) were tested using the *caret* package (Kuhn 2008) in R

before final prediction RFs were created. Values of *mtry* tested included 1 through *m* (the

total number of independent variables). Different values of *ntree* were also tested against

model performance and included 50 through 100 in intervals of 10, 100 through 1000 in

intervals of 100, and 1,000 through 20,000 in intervals of 1,000. These intervals were

chosen because error decreases exponentially, so adding trees to an already large forest

will not produce the same amount of improvement as adding the same number of trees to a small forest. As well, using larger intervals as the number of trees increases (i.e. 10 to 100 to 1,000) is significantly less time consuming than staying with the same interval for all sizes of forest. The maximum *ntree* value (20,000) was chosen based on the *ntree* used for variable importance procedures. Values of *mtry* and *ntree* used in prediction RFs were those that resulted in the lowest standard deviation on model prediction errors (RMSEs) using out-of-bag (OOB) samples (Breiman 2001). An OOB RMSE can be generated each time a tree is created, which makes this method helpful when choosing final values of *mtry* and *ntree*. To validate prediction RFs, predictions were made using species from the validation set (n = 6 species), and plots of predicted versus observed RMRs were created. A prediction was considered a pass only if it was within ± 10% of the observed value, and four passing predictions of six were required for the models to be considered successful. The "predict" function in R was used to make all RF predictions.

RESULTS

Metabolic Rate Data

RMR data were collected for 66 species of fish, not including species left out due to significant borrowing of parameter values from other species. For instance, the parameter set for Pink Salmon *Oncorhynchus gorbuscha* (Beauchamp *et al.* 1989) is very similar to that of Sockeye Salmon *Oncorhynchus nerka* (Beauchamp *et al.* 1989), so Sockeye Salmon was not used. RMRs ranged from 1.2E-3 to 1.75E-2 g $O_2 \cdot$ g fish$^{-1} \cdot$ d^{-1}. The mean ± SD rate was 4.7E-3 ± 2.8E-3 g $O_2 \cdot$ g fish$^{-1} \cdot$ d^{-1}. The dataset included representation from 21 of the 33 families of freshwater, north-temperate fish species in

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North America, plus representation from 2 families not yet established in north-temperate

North America (Channidae and Eleotridae). The 12 families not represented (Amiidae,

Atherinopsidae, Characidae, Cichlidae, Embiotocidae, Fundulidae, Hiodontidae,

Lepisosteidae, Loricariidae, Percopsidae, Sciaenidae, and Syngnathidae) tended to

contain low numbers of species (range 1 to 5 species). Within families, there was an

average of 30% representation, ranging from 0-100%.

Fish Traits used to Predict RMR

In total, 5 categorical and 18 continuous, independent variables were analyzed.

Of the categorical variables, levels ranged from 2-4 and were chosen based on levels used

by the sources from which the data were collected. Within the MP variable, terminal and

superior were grouped as one level to facilitate ease of use of the final model, as it is

often difficult to discriminate between the two mouth types. Since much field work is

conducted by individuals still learning the trade (i.e. students, recent graduates), with

experts spending large amounts of time away from the field due to requirements of

supervisory positions, ease of model application is essential. The same reasoning was

applied for grouping benthopelagic and pelagic as one level within the HP variable, as

well as for grouping carangiform and sub-carangiform as one level within the ST

variable. Also within the ST variable, labriform and diodontiform were grouped as one

level because each is a swimming type dependent on pectoral fins. Of the 23 independent

variables, 4 of 11 body measurements (PA, PPEL, PPEC, and CA) as well as K were only

used in the subset analysis due to limited data availability. Figures 3.1 and 3.2 show

relationships between each continuous, independent variable. Figure 3.1 is based on the

main training set data (n = 60 species) and Figure 3.2 is based on the subset (n = 49 species). Figure 3.2 includes only variables not analyzed in Figure 3.1. As indicated in Figures 3.1 and 3.2, one or two extreme points were observed in RMR, AM, MW, MTL, HL, ML, MF, K, PA, PPEC, and CA, although since statistical procedures used in the current research were all non-parametric, there was no need to perform outlier tests. Figures 3.3 and 3.4 show distributions of each continuous, independent variable.
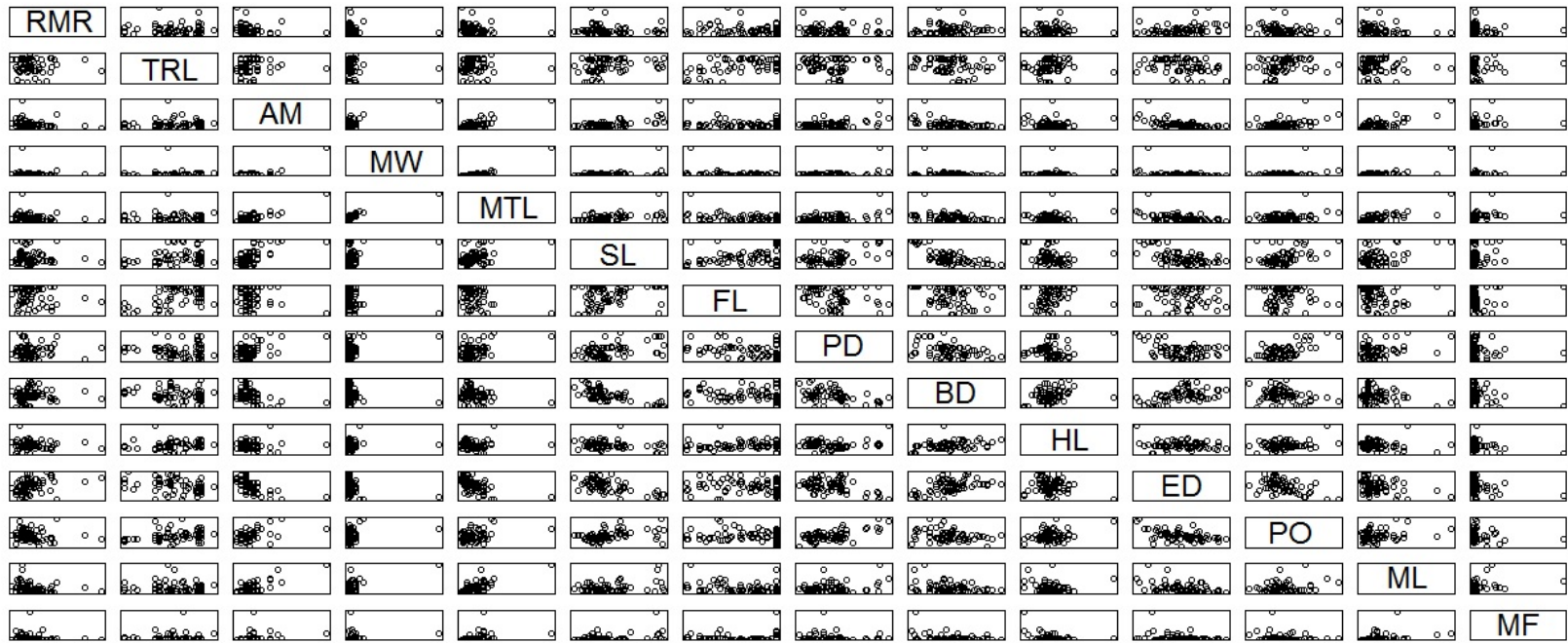
Figure 3.1. Relationships between routine metabolic rate (RMR; g O$_2$ • g fish^{-1} • d^{-1}) and a number of traits from 66 species of freshwater (and highly anadromous), north-temperate ($\geq$ 40°N latitude) fish species analyzed for relationships with RMR. X-axes of plots correspond with the trait occurring in the same column. Y-axes of plots correspond with the trait occurring in the same row. TRL=trophic level, AM=age at maturity (years), MW=maximum weight (g), MTL=maximum total length (mm), SL=standard length to total length ratio (%), FL=fork length to total length ratio (%), PD=pre-dorsal length to total length ratio (%), BD=body depth to total length ratio (%), HL=head length to total length ratio (%), ED=eye diameter to head length ratio (%), PO=pre-orbital length to head length ratio (%), ML=maximum lifespan (years), and MF=maximum fecundity (number).
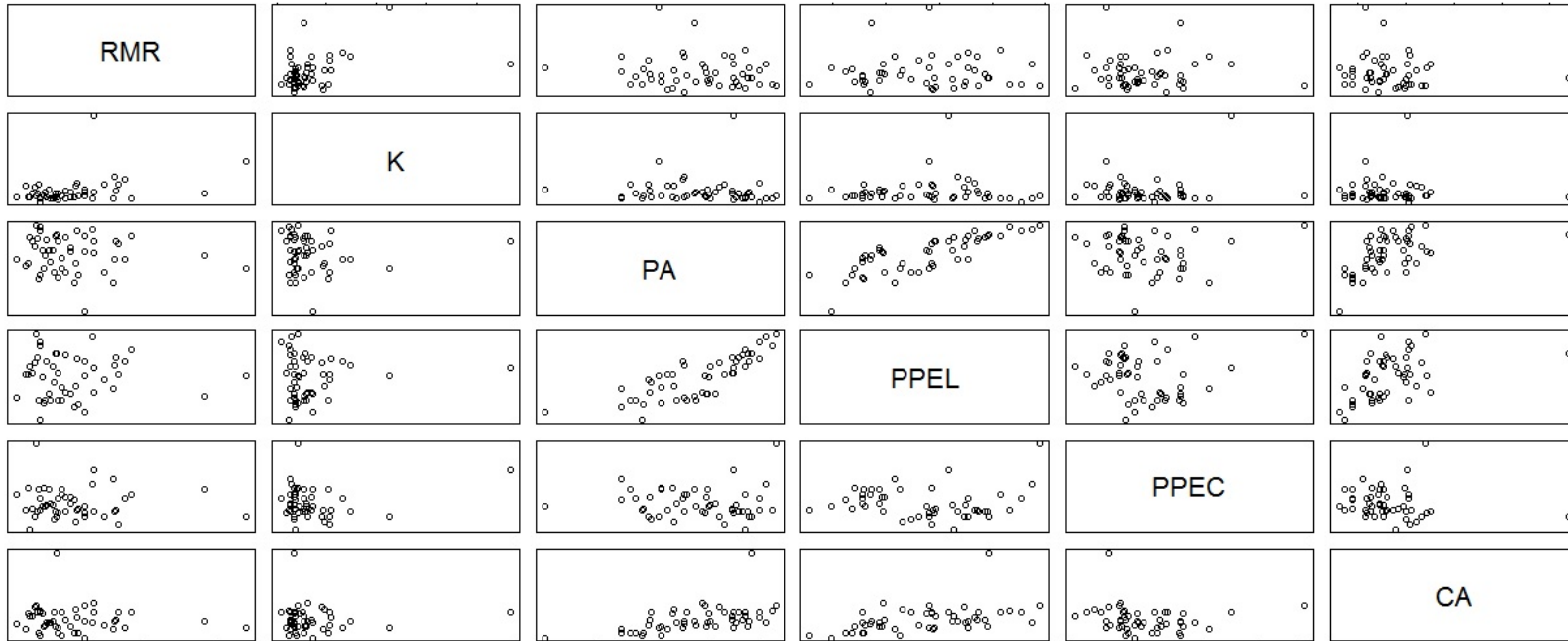
Figure 3.2. Relationships between routine metabolic rate (RMR; g O_2 • g fish^{-1} • d^{-1}) and a number of traits from 49 species of freshwater (and highly anadromous), north-temperate ($\geq$ 40°N latitude) fish species analyzed for relationships with RMR. X-axes of plots correspond with the trait occurring in the same column. Y-axes of plots correspond with the trait occurring in the same row. K=von Bertalanffy growth coefficient (cm • year^{-1}), PA=pre-anal length to total length ratio (%), PPEL=pre-pelvic length to total length ratio (%), PPEC=pre-pectoral length to total length ratio (%), and CA=caudal aspect ratio.
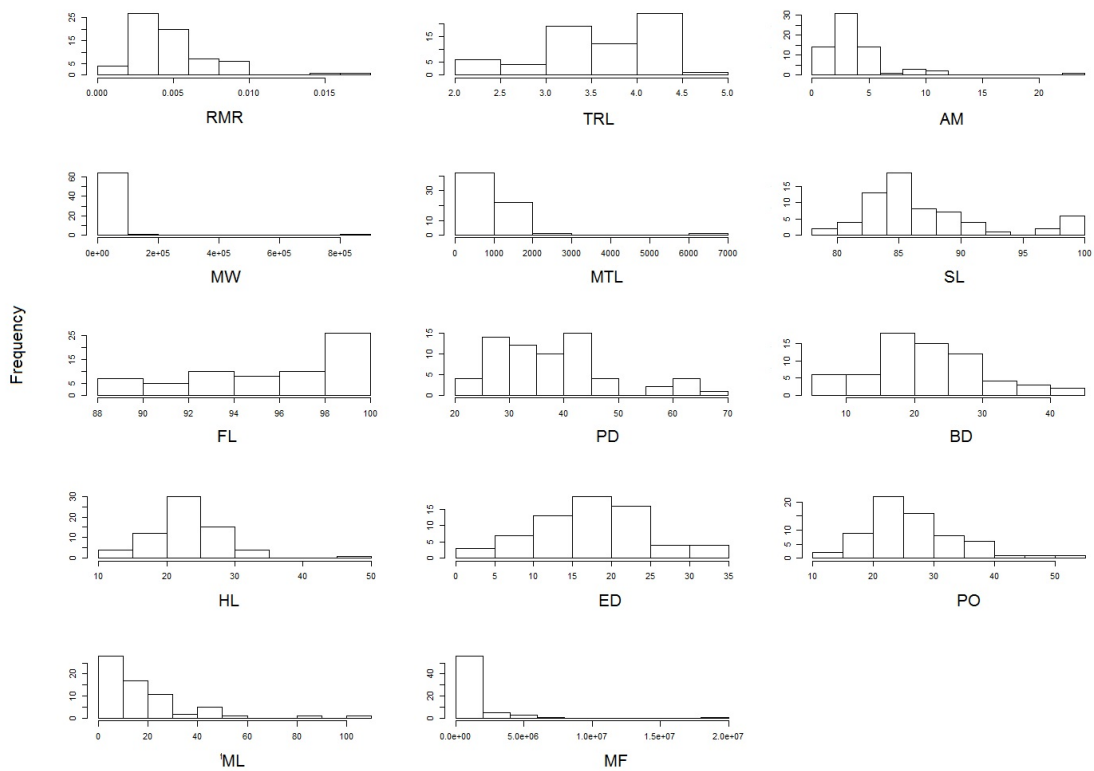
Figure 3.3. Distributions of routine metabolic rate (RMR; g O_2 • g fish^{-1} • d^{-1}) and a number of traits from 66 species of freshwater (and highly anadromous), north-temperate (≥ 40°N latitude) fish species analyzed for relationships with RMR. TRL=trophic level, AM=age at maturity (years), MW=maximum weight (g), MTL=maximum total length (mm), SL=standard length to total length ratio (%), FL=fork length to total length ratio (%), PD=pre-dorsal length to total length ratio (%), BD=body depth to total length ratio (%), HL=head length to total length ratio (%), ED=eye diameter to head length ratio (%), PO=pre-orbital length to head length ratio (%), ML=maximum lifespan (years), and MF=maximum fecundity (number).
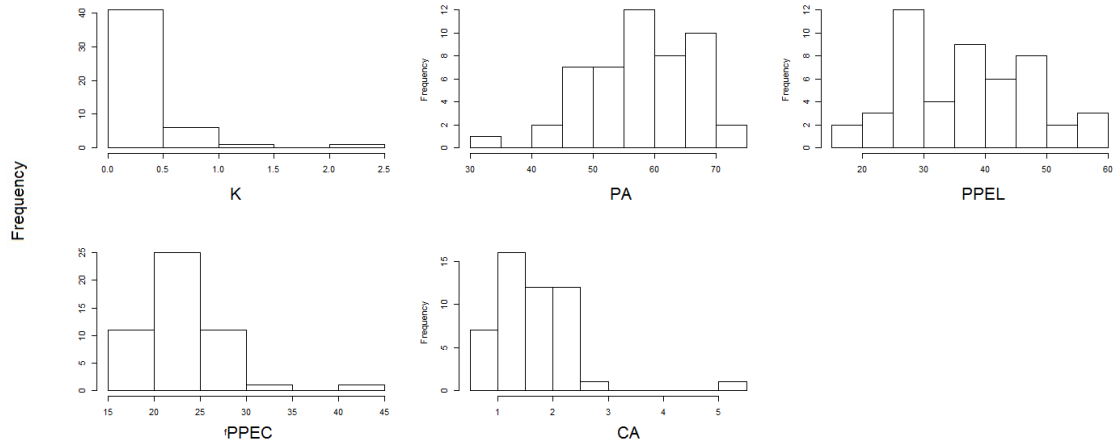
Figure 3.4. Distributions of a number of traits from 49 species of freshwater (and highly anadromous), north-temperate ($\geq$ 40°N latitude) fish species analyzed for relationships with routine metabolic rate. K=von Bertalanffy growth coefficient (cm • year^{-1}), PA=pre-anal length to total length ratio (%), PPEL=pre-pelvic length to total length ratio (%), PPEC=pre-pectoral length to total length ratio (%), and CA=caudal aspect ratio.

Prediction of RMR from Fish Traits

When RMRs were categorized, AM, ML, MW, ED, TG, and MTL were considered important in the main training set analysis using the method of Strobl *et al.* (2009b). Note traits are not listed in any particular order due to slight variation in importance rank throughout trials. K and AM were considered important in the subset analysis. In the reduced sets analysis, AM and MTL were important in all ten, ML was important in nine, and ED was important in seven

When RMRs were left as continuous values, TG, AM, MTL, ED, and ML were considered important in the main training set analysis; and the same variables, excluding TG but including K, were considered important in the subset analysis. In the reduced sets analysis, AM and ED were important in all ten, and MTL was important in seven.

When validated, both CTs (main training set CT, Figure 3.5; reduced set CT, Figure 3.6) failed to meet passing criteria. Both the main training set CT and reduced set CT classified three of six species correctly.
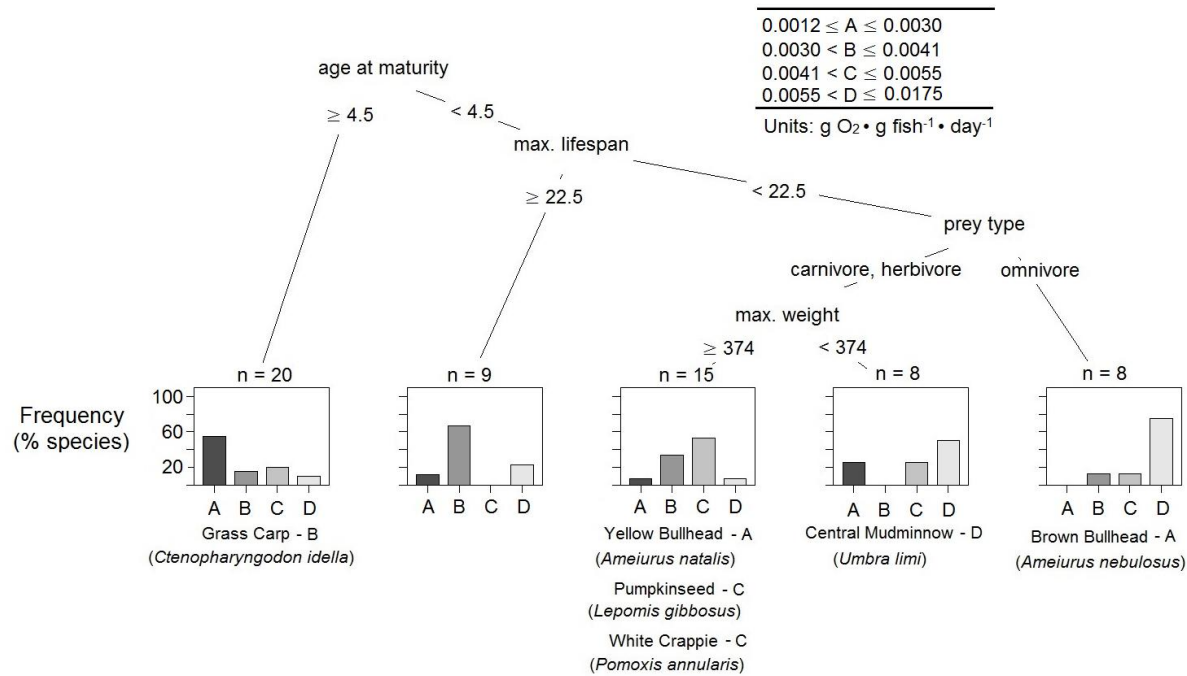
Figure 3.5. Classification tree (*rpart* (Therneau *et al.* 2015) package in R, plotted with *partykit* (Hothorn and Zeileis 2015) package in R, set.seed(1)) to predict routine metabolic rate (RMR) from 60 freshwater (and highly anadromous), north-temperate ($\geq 40°$N latitude) fish using six independent variables (determined important in describing RMR by random forest procedures) related to morphology, physiology, and ecology. Results of validation using six fish withheld from the dataset used to train the model are shown. Validation species are placed below RMR boxes into which they were classified when run through the CT. Letters beside species' names represent actual RMR categories based on listing all 66 species in asceding order of RMR and dividing into four groups based on quartiles (A, B, C, and D). A failed classification is one in which actual species category does not match the category with the tallest bar in the box in which the species was classified, as bars represent frequency of species from the training data belonging to each category. Passing criteria was four successful classifications out of six.

Figure 3.6. Classification tree (*rpart* (Therneau *et al.* 2015) package in R, plotted with *partykit* (Hothorn and Zeileis 2015), set.seed(1)) to predict routine metabolic rate (RMR) from 60 freshwater (and highly anadromous), north-temperate ($\geq 40°$N latitude) fish using four independent variables (determined important in describing RMR by random forest procedures) related to morphology and physiology. Results of validation using six fish withheld from the dataset used to train the model are shown. Validation species are placed below RMR boxes into which they were classified when run through the CT. Letters beside species' names represent actual RMR categories based on listing all 66 species in asceding order of RMR and dividing into four groups based on quartiles (A, B, C, and D). A failed classification is one in which actual species category does not match the category with the tallest bar in the box in which the species was classified, as bars represent frequency of species from the training data belonging to each category. Passing criteria was four successful classifications out of six.

As mentioned previously, RFs require tuning of parameters (*mtry* and *ntree*) to ensure optimal predictive capability. Using only variables important in the main training set analysis, values of *ntree* and *mtry* resulting in the lowest RMSE (2.42E-3) using the OOB method were 100 and 5, respectively. Therefore, these values were used in the main training set prediction RF. The maximum RMSE (2.60E-3) using the OOB method occurred when *ntree*=2,000 and *mtry*=1. Figure 3.7 indicates observed versus predicted RMRs for six species of fish used to validate the main training set prediction RF. Using only variables important in at least seven of ten reduced sets, values of *ntree* and *mtry* resulting in the lowest RMSE (2.47E-3) using the OOB method were 100 and 2, respectively. Therefore, these values were used in the reduced set prediction RF. The maximum RMSE (2.51E-3) using the OOB method occurred when *ntree*=90 and *mtry*=1. Figure 3.8 indicates observed versus predicted RMRs for six species of fish used to validate the reduced sets prediction RF. When validated, both RFs failed to meet passing criteria. The main training set RF had two passing predictions, while the reduced set RF had one. Figures 3.9 to 3.12 display the relationships between predicted and observed OOB (Figures 3.9 and 3.10) and in-bag (IB; Figures 3.11 and 3.12) routine metabolic rates.
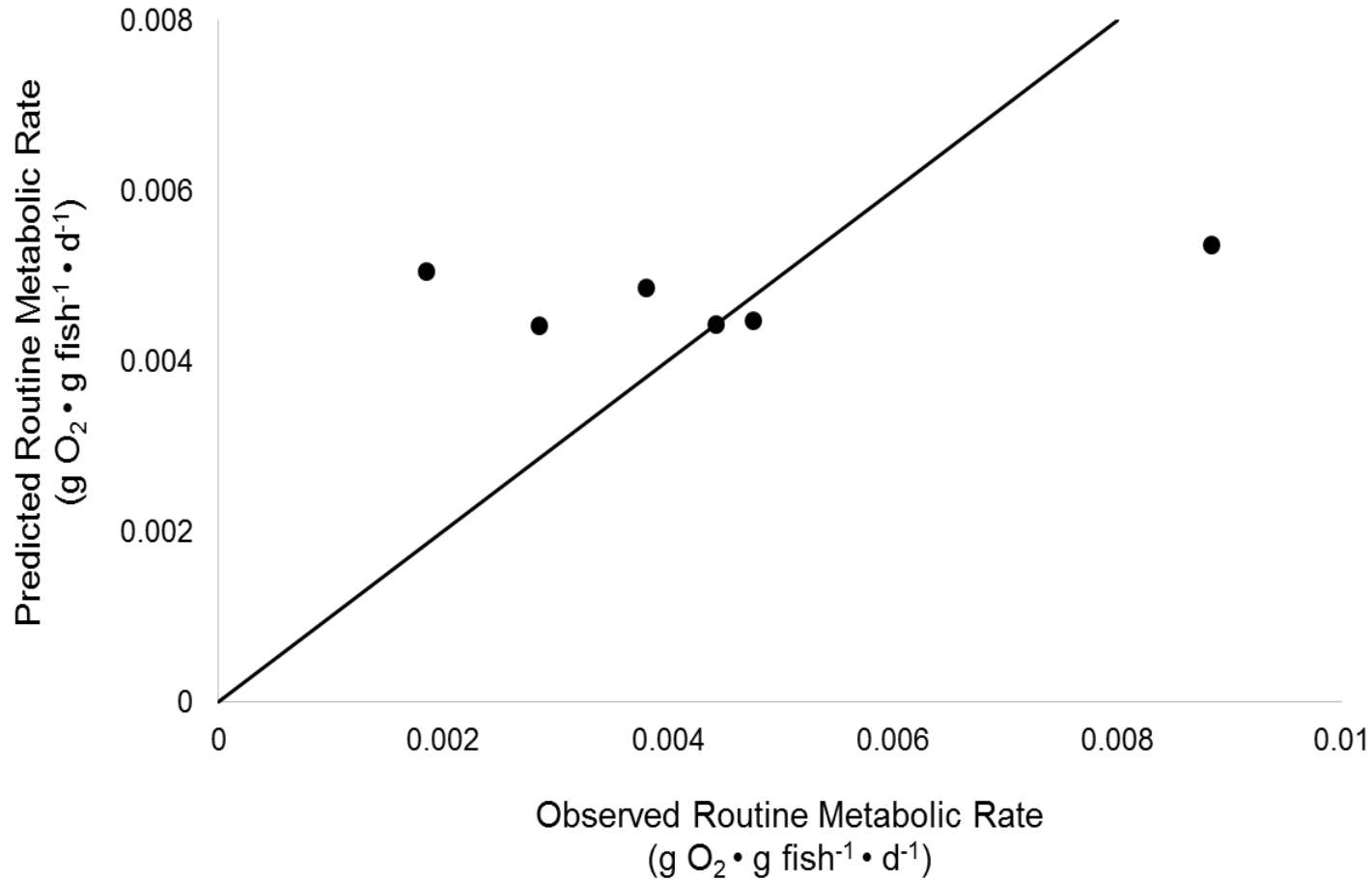
Figure 3.7. Predicted versus observed routine metabolic rates of six species of freshwater, north-temperate (≥ 40°N latitude) fish used to validate a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of 60 species and five traits (prey type, age at maturity, maximum total length, eye diameter to head length ratio, and maximum lifespan). The line indicates the 1:1 (predicted:observed) relationship, which the points would have followed had the random forest made successful predictions.
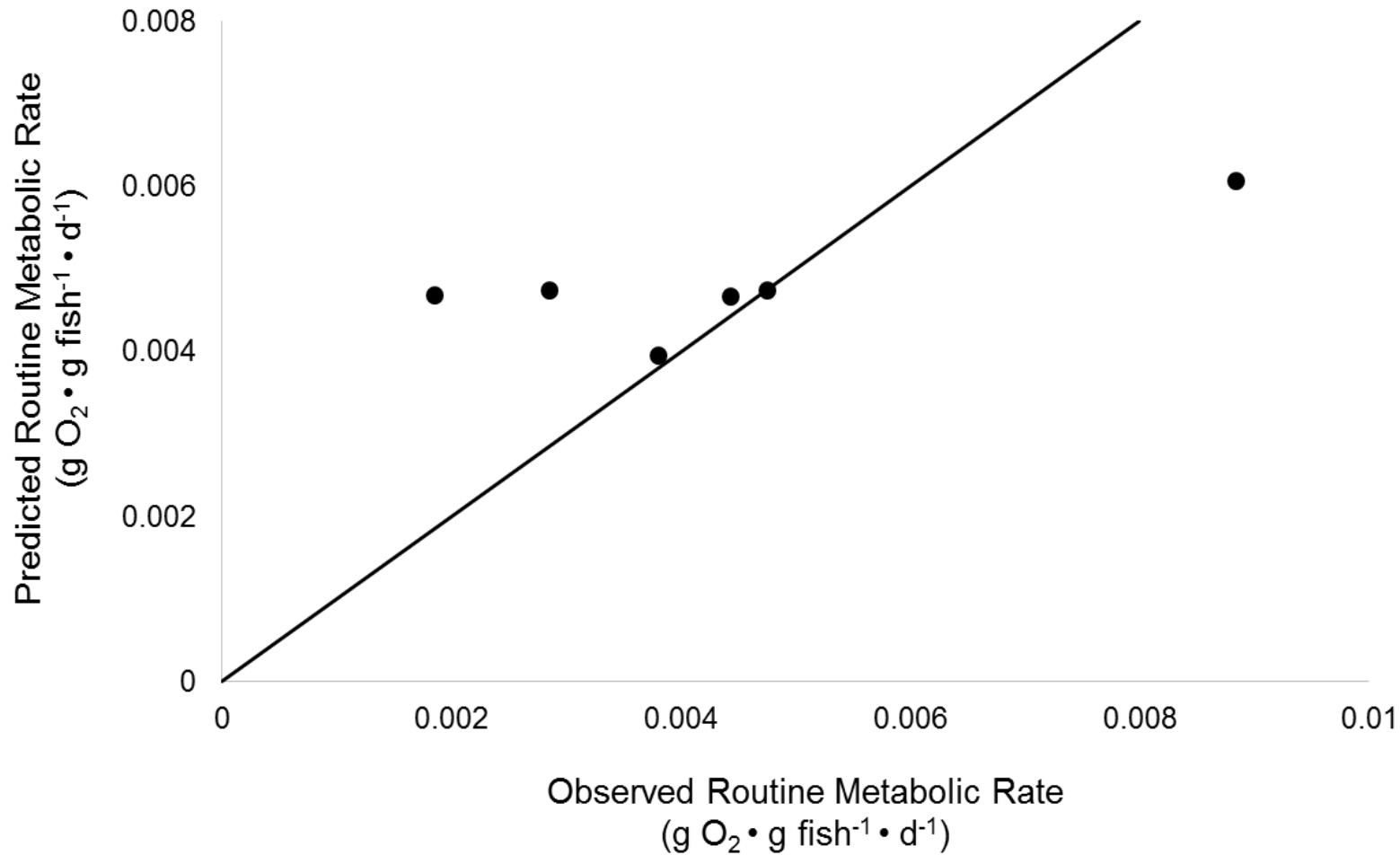
Figure 3.8. Predicted versus observed routine metabolic rates of six species of freshwater, north-temperate ($\geq 40°$N latitude) fish used to validate a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of 60 species and three traits (age at maturity, maximum total length, and eye diameter to head length ratio). The line indicates the 1:1 (predicted:observed) relationship, which the points would have followed had the random forest made successful predictions.
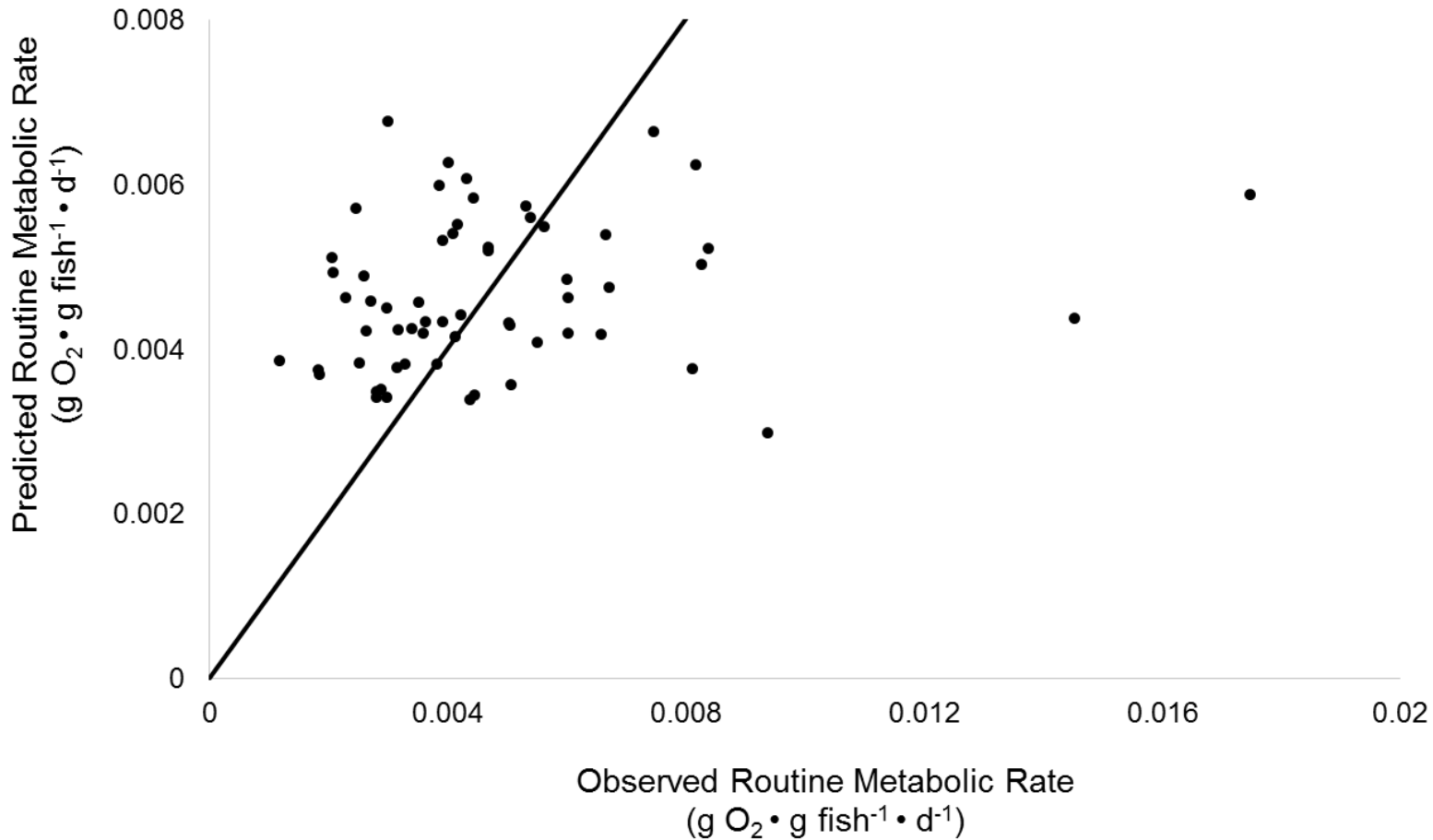
Figure 3.9. Out-of-bag (Breiman, L. 2001. Random forests. Machine Learning 45:5-32) predicted versus observed routine metabolic rates of 60 species of freshwater, north-temperate ($\geq 40°N$ latitude) fish from a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of the same 60 species as well as five traits (prey type, age at maturity, maximum total length, eye diameter to head length ratio, and maximum lifespan). The line indicates the 1:1 (predicted:observed) relationship.
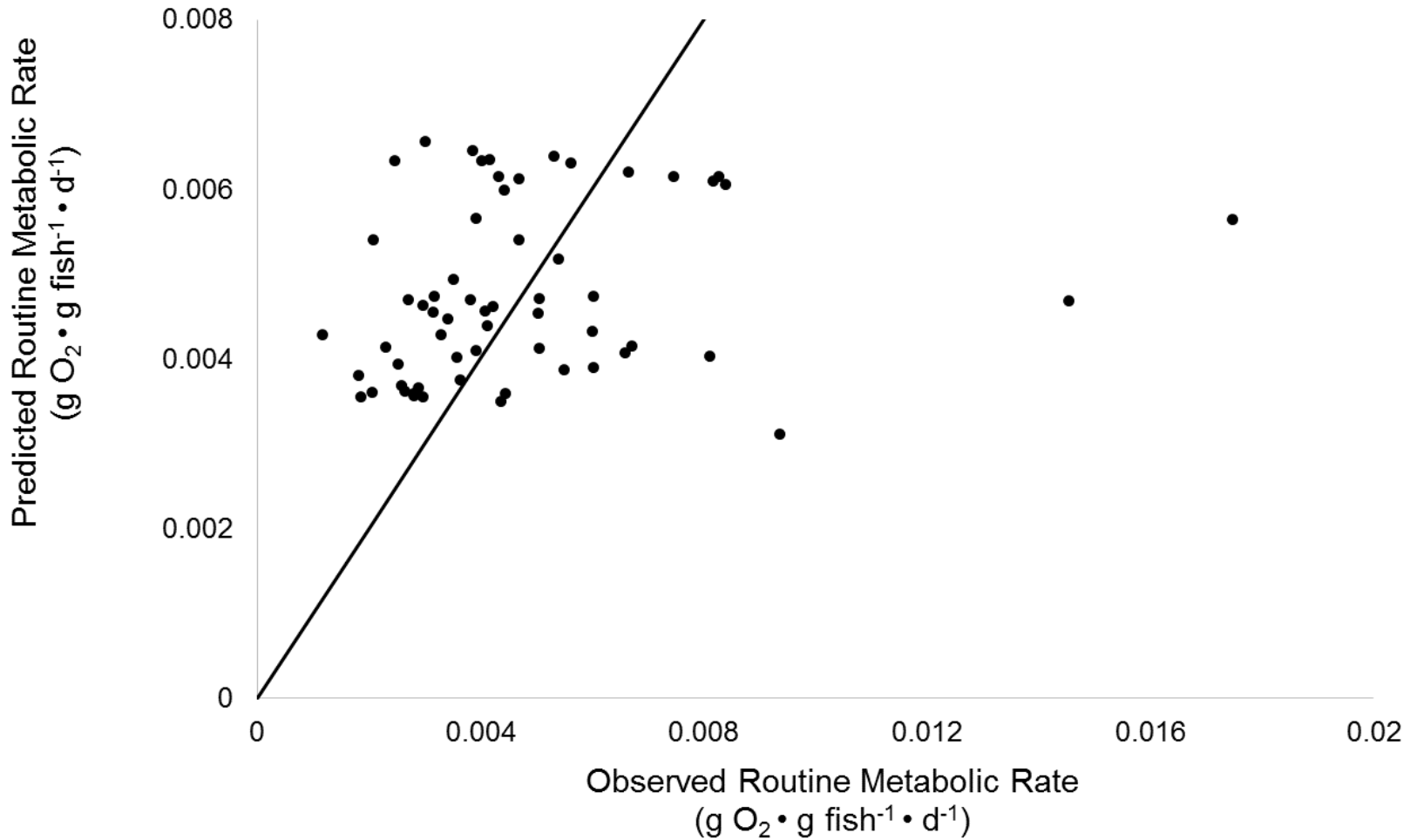
Figure 3.10. Out-of-bag (Breiman, L. 2001. Random forests. Machine Learning 45:5-32) predicted versus observed routine metabolic rates of 60 species of freshwater, north-temperate (≥ 40°N latitude) fish from a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of the same 60 species as well as three traits (age at maturity, maximum total length, and eye diameter to head length ratio). The line indicates the 1:1 (predicted:observed) relationship.
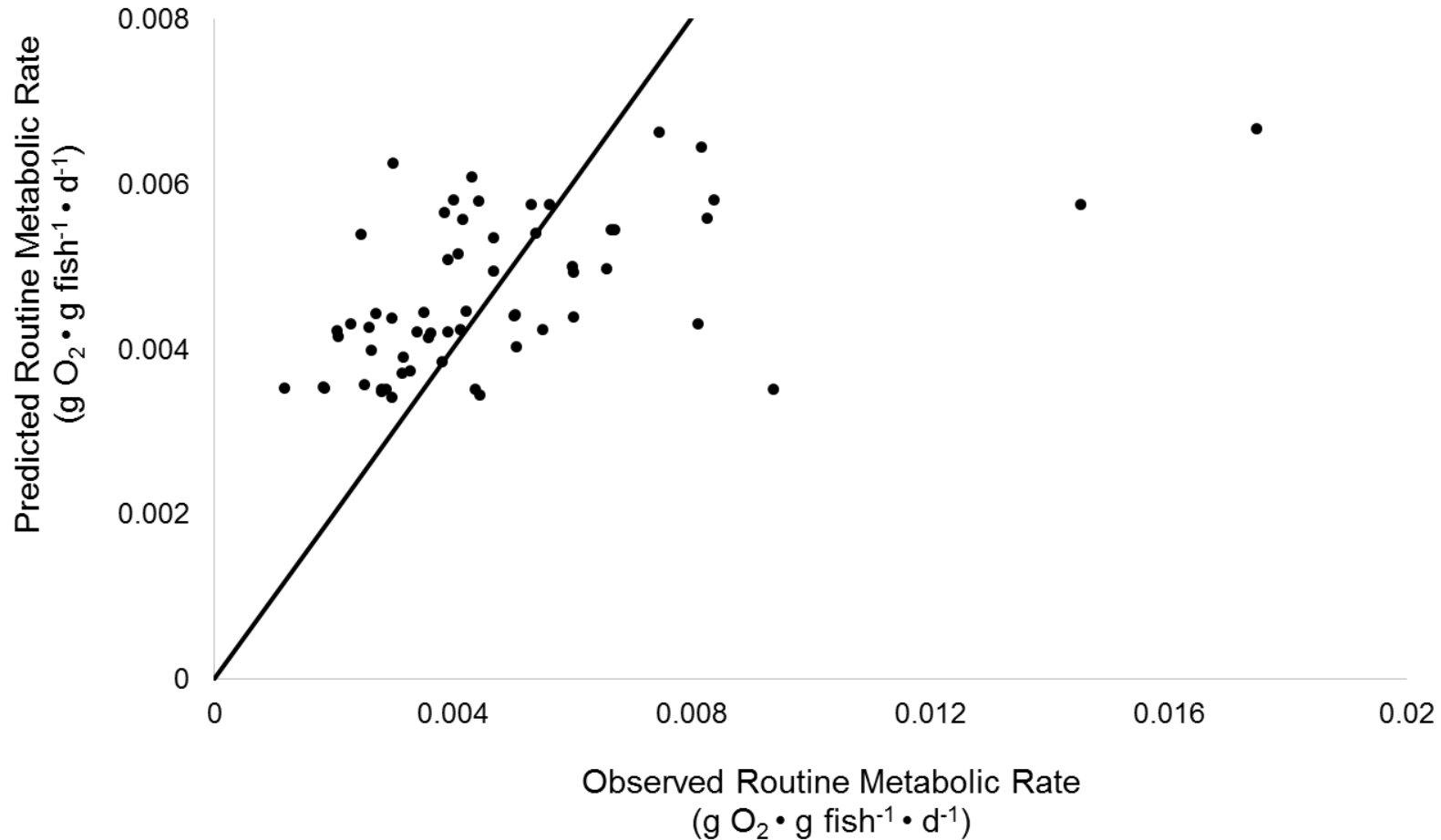
Figure 3.11. In-bag (Breiman, L. 2001. Random forests. Machine Learning 45:5-32) predicted versus observed routine metabolic rates of 60 species of freshwater, north-temperate ($\geq 40°N$ latitude) fish used to train a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of the same 60 species as well as five traits (prey type, age at maturity, maximum total length, eye diameter to head length ratio, and maximum lifespan). The line indicates the 1:1 (predicted:observed) relationship.
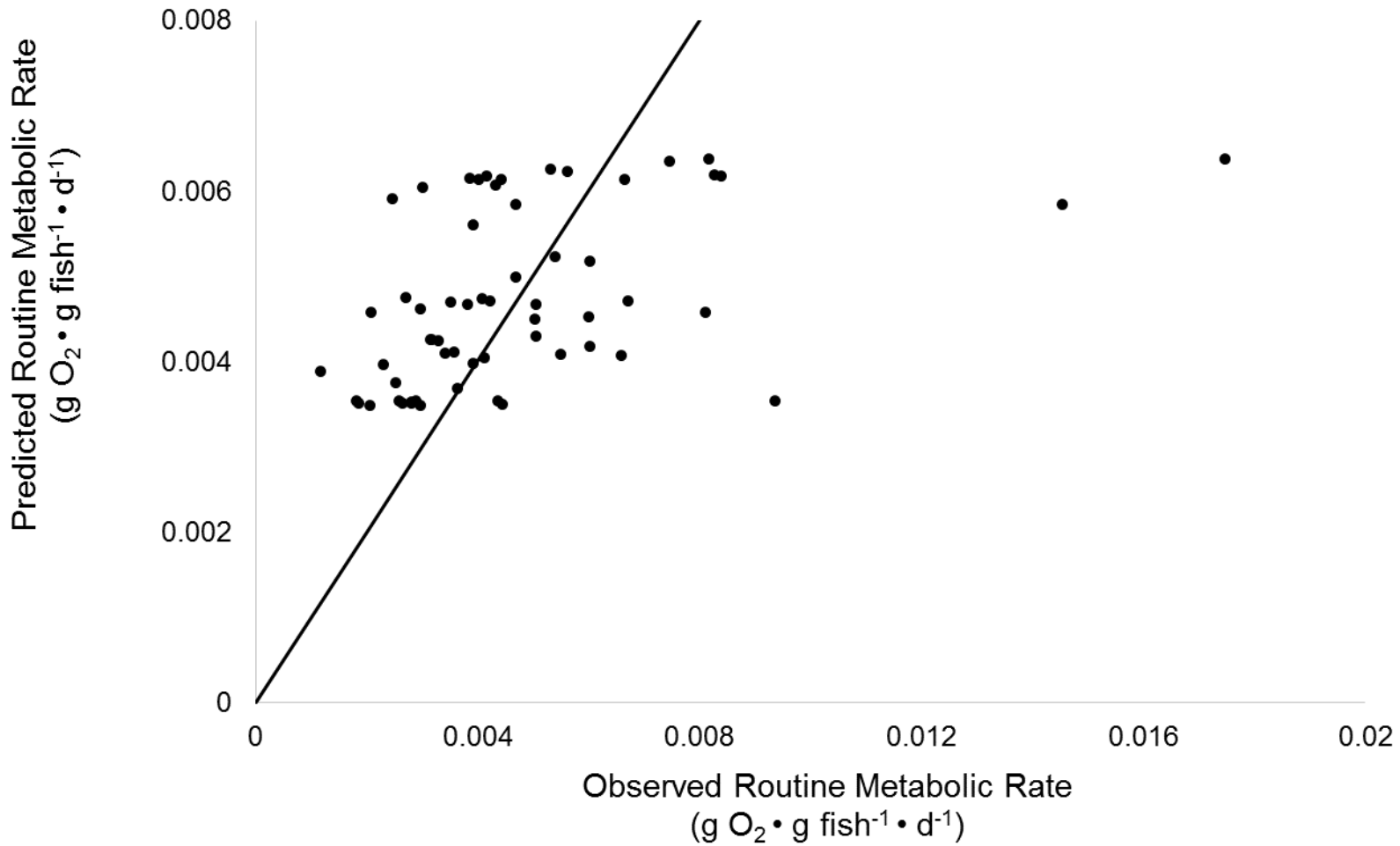
Figure 3.12. In-bag (Breiman, L. 2001. Random forests. Machine Learning 45:5-32) predicted versus observed routine metabolic rates of 60 species of freshwater, north-temperate ($\geq$ 40°N latitude) fish used to train a random forest created to predict rates of freshwater (and highly anadromous), north-temperate fish from analysis of the same 60 species as well as three traits (age at maturity, maximum total length, and eye diameter to head length ratio). The line indicates the 1:1 (predicted:observed) relationship.

DISCUSSION

All CT and prediction RF models created in the current research did not meet passing criteria when validated, yet criteria for both CTs would have been met if one more species had been properly classified in each. Six validation species is a small sample size. Rerunning CT validation procedures using more validation samples would provide a stronger analysis of predictive capability, and the same may be said for the RFs. RF models predicted little variation relative to observed values, but analyses of predicted versus observed OOB samples for both RFs (Figures 3.9 and 3.10) indicate stronger relationships than those shown in Figures 3.7 and 3.8.

Fish Traits

Three independent variables were consistently determined important in the current analysis: AM, MTL, and ED. K was determined important in both subset analyses and, as such, should be collected for a greater number of fish species. From the plots and histograms presented in Figures 3.1 through 3.4, it appears ED is normally distributed, but AM, MTL, and K are all skewed right with possible outliers. RFs do not require normal distributions because this is not an assumption of the CTs of which they are composed (Cutler 2010), and RFs are also quite robust to outliers (Breiman 2001). Therefore, the shape of distributions and presence of outliers likely had little effect on predictions. The current research was unable to provide reasons for why ED may be related to RMR. Body mass, however, is a strong contributor to RMR, since RMR is strongly related to allometry (Kleiber 1932). Of the independent variables found consistently important, AM, MTL, and K all relate to allometry. In fish, maturity is

reached once a certain body mass has been obtained and may be delayed in terms of age if body mass requirements are not met (Rowe and Thorpe 1990). MTL is naturally expected to correlate with MW, and K describes change in body mass. As such, although these three variables may not produce the same results if substituted for each other in a CT or RF, they all relate to allometry, which research has already identified as being something that influences RMR. Similarly, research has identified water temperature as being a strong contributor to RMR (Kitchell *et al.* 1977; Stewart *et al.* 1983). RMRs used in the current analysis were those experienced by each species at their FTPs, so inclusion of FTP as an independent variable would have caused autocorrelation. However, thermal regime (cold-, cool-, and warm-water) could have been used as an independent variable to account for contribution of temperature to RMR, but this was overlooked.

In addition to adding thermal regime as an independent variable, traits related to gill morphology may have been useful in the current analysis, although data on gill morphology is not easily available for a large number of species. The main areas of gas exchange in fish species are the lamellae in gills. Hughes (1966) found gill designs in active fish species facilitate limited flow resistance through longer gill filaments and more secondary folds than in sedentary fish species. Hughes also found more active species typically have larger gill areas than sedentary species, a conclusion supported by a recent review by Clark *et al.* (2013).

It was peculiar that CA was not among the traits found to be important in describing RMR, as Palomares and Pauly (1998) had indicated a relationship between CA and food consumption. The work of Palomares and Pauly (1998) only included 65

species of fish, although many species were represented multiple times, as these

researchers used fish populations as their units of study. In total, the research of

Palomares and Pauly (1998) included 108 samples, which is a sample size approximately

44% greater than that of the current research (n = 60 species). The larger sample size

would have provided more statistical power in the work of Palomares and Pauly (1998).

As well, these researchers included both freshwater and marine species, which may have

facilitated greater morphological variation within their dataset than the dataset used in the

current research. Finally, and most likely, there is question as to the precision of the

RMR data used in the current research (see "Scrutinizing RMR Measures" section).

Scrutinizing RMR Measures

Emphasis has been placed on ensuring sources of error in respirometry trials are

addressed (Steffensen 1989), as many factors may contribute to imprecisions in

measurements (Brett 1962) such as variations in water salinity, oxygen availability, and

duration for which fish are fasted. In fact, SDA can play a large role in influencing

RMR. Jobling and Davies (1980) found that SDA in Plaice *Pleuronectes platessa*

elevated metabolic rates up to twice resting levels, that effects of SDA lingered for up to

three days, and that SDA increased with meal size. Beamish (1974) found the time it

takes metabolic rates in Largemouth Bass *Micropterus salmoides* to reach pre-feeding

levels was dependent not only on meal size, but also on fish weight, with more time

required for larger fish. Jobling and Davies (1980) found SDA was highest in Plaice after

consumption of protein-rich food. Similarly, Carter and Brafield (1992) found SDA in

Grass Carp *Ctenopharyngodon idella* was greatest after consuming a high-protein diet, followed next by a high-carbohydrate diet, and then finally a high-fat diet.

Although researchers go to great lengths to control for the various factors affecting RMR, it is recognizable that control measures may not be applied in the same way from one study to another. Standardized approaches applied to the numerous sources of variability would ensure measurements are equivalent in terms of how they are obtained. This variability is of particular interest in the current research because similar species, such as Brown and Yellow Bullhead, which would naturally be predicted to have similar RMRs based on similarity in morphology, physiology, and ecology, had RMRs differing by a wide margin. The RMR of Brown Bullhead was only 65% that of Yellow Bullhead. Further, the RMR of Japanese Eel *Anguilla japonica* was only 61% that of American Eel *Anguilla rostrata*, and the RMR of Bighead Carp *Hypophthalmichthys nobilis* was only 34% that of Silver Carp *H. molitrix*. Such scrutinizing of RMR data can be helpful in screening potentially imprecise measures and should be of priority in future work, but there is question as to how far apart similar species must be in terms of RMR to warrant speculation.

Effects of Taxonomy

Clark and Johnson (1999) showed there is more variation in oxygen consumption among than within fish families. This finding is not surprising, since more variation in morphology, physiology, and ecology is expected to occur among than within families. Many traits are related to RMR, as discussed, so the more traits shared by two fish species, the closer their RMRs. Instead of comparing at the species level, comparisons

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could be made at the family level to address the findings of Clark and Johnson (1999). Using family-level comparisons, traits could be chosen so as to differentiate between families as well as describe RMR. However, the focus of this research was on the species-level, which would have facilitated more taxonomically-specific tools than focusing on the family-level had the tools performed well. If successful tools were focused on the family-level, they would only be of use when comparing species in different families.

Activity Multipliers

Winberg (1956) suggested using a factor of 2 for adjusting SMR to a RMR. However, Ware (1975) suggested a factor of 3 for young, actively growing Bleak *Alburnus alburnus* under normal feeding conditions, but a factor of 2-2.5 when food supply is better than normal, which indicates activity costs due to foraging may not be easily defined. Metabolic work by Kerr (1971a, 1971b, 1971c) assumed natural selection aims to create optimal growth to food consumption ratios, supporting the suggestion of Ware (1975) to take food supply into account when estimating activity. In addition, environment should also be taken into account. Fish of a given species living in fast moving waters typically have higher oxygen consumption rates than fish of the same species living in calm waters (Clausen 1936). In the current research, activity multipliers were estimated for 14 species in the main training set and 2 in the validation set (i.e. not part of the main training set). Activities of all fish for which non-linear fits were created were estimated, but in many cases (not included in the previously mentioned 14), laboratory studies had determined RMR as opposed to SMR. In these cases, activity

multipliers were not used to scale data from standard to routine levels, as levels were already routine, but were simply used to promote better estimates of other parameters (i.e. not confounded by activity). Activity multipliers were based on values for similar species for which activity has already been described. For instance, along with some laboratory studies producing measures for fish species at SMR, thus requiring addition of activity, Hanson *et al.* (1997) and other literature provide parameters specifically for RMR. However, borrowing activity multipliers does not guarantee accuracy, especially considering the large effects activity can have on metabolic rate. Using multipliers from similar species may also nullify effects activity may really have in terms of differentiating RMR between species.

Place of Food Consumption Analyses in AIS Management

The current research focused on trophic impact through FCR, using RMR as a surrogate. Although FCR is one thing managers should consider when making AIS management decisions, other factors, both biotic and abiotic, will play a role in the overall impact a species has. Parker *et al.* (1999) suggested AIS impact is comprised of three components and can be stated in terms of the equation:

$$I = R \cdot A \cdot E$$

where I is total impact, R is the range size of the invader, A is invader abundance, and E is the impact of a single individual from the invading species. The current research is one component of what Parker *et al.* (1999) denoted "E". Many other factors, such as parasitism, hybridization, niche displacement, behaviour change in native species, and introductions of new diseases play important roles in impact. To make assumptions

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based on impact AIS may have if introduced, other factors within E, as well as R and A, should be addressed. Although R and A will be small for newly arrived species in a system, if E is equal between the two species, R and A will be factors differentiating between eventual I of each.

Olden *et al.* (2006) looked at invasions and extirpations in the Colorado River Basin and suggested native species most susceptible to extirpations are those with similar life-histories as invaders, and extirpation-prone native species are often not as adapted as non-native species to conditions resulting from anthropogenic change (in Olden's case, warm, slow-moving water). The research of Olden *et al.* (2006) suggested the impacts invaders have will depend not only on invader characteristics, but also on native species characteristics and how anthropogenically modified recipient ecosystems are. Examination of native species' characteristics is not novel. Reynolds *et al.* (2005) examined threatened fish species and fish species with low risk of extinction in Europe. Among the results, they found threatened, freshwater species tend to have smaller body size, but this relationship was the opposite when anadromous species were examined. In addition, they found threatened species were restricted to lower latitudes and typically occupied a narrower variety of habitat types. Similarly, ecological specialization among extirpated species was a finding of work by Angermeier (1995), who examined ecological specialization among extirpated species and also concluded multiple anthropogenic stressors, rather than isolated factors, contributed to extirpations. The findings Olden *et al.* (2006), Reynolds *et al.* (2005), and Angermeier (1995) bring to light the importance of studying not only invader traits in AIS management, but also native species' traits and habitat characteristics.

Future Work

Although the current research failed to produce a predictive tool for AIS trophic

impact screening, this analysis has identified a number of issues that should be addressed

to facilitate better results in future work. First, a larger validation set is needed to

adequately assess predictive capabilities of CTs and RFs, as both CTs were only one

successful classification away from being deemed useful. Second, emphasis should be

placed on collecting data for AM, MTL, ED, and K, since these traits were found

consistently important in describing RMR. In addition, data collection should focus on

traits related to thermal regime and gill morphometry. Third and probably of greatest

priority, emphasis must be placed on scrutinizing RMR measures, as the current research

displayed instances in which very similar species (e.g. Yellow and Brown Bullhead) had

RMR values differing by wide margins. However, there is question as to how far apart

similar species should be in terms of RMR to warrant speculation as well as how similar

species must be in order to be classified as similar. Many factors confound results of

respirometry trials and must be controlled to obtain precise measures, but even when

control measures are optimal, it is recognizable they may not be applied in the same

fashion from one study to another. Collaboration between researchers to standardize

methods would help in this area. Fourth, to address the findings of Clark and Johnson

(1999), comparisons should be made at the family-level as opposed to the species-level.

Traits presumed to differentiate between families as well as describe RMR could be of

focus when conducting similar studies. However, predictive tools based on the family-

level would only be useful if species being compared are in different families. Fifth, little

is known about the activities of various species under normal conditions in the wild, and

activity can vary depending on habitat. As such, SMR may be an easier measure to use than RMR, but metabolic rate incorporating zero activity does not provide an accurate measure of energy use under normal conditions, since fish are not sedentary all the time. More understanding of activity is needed. Again, generalizing to the family-level may help in this case, as it would be easier to simply say one family is generally more active than another. Last, the current research represents only a portion (trophic impact) of what is understood as impact and should be used in conjunction with research pertaining to potential range and abundance of the invader, other impact measures (parasitism, hybridization, niche displacement, behavior change in native species, introductions of new diseases, etc.), and characteristics of native species and environmental conditions in the recipient system.

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CHAPTER 4

GENERAL DISCUSSION

The case-histories and case-studies analyzed in Chapter 2 provided evidence that invasive fish species have higher bioenergetic rates than native fish species with which they coexist. However, bioenergetic rates within a species can vary considerably from one location to another due to differences in water temperature, fish behaviour, diet, habitat suitability, etc. This variation makes it difficult to generalize bioenergetic rates for a given species. As such, Chapter 3 of this thesis relied on metabolic rate data gathered from lab studies in which environmental variables were controlled. Although variation in routine metabolic rate (RMR) was observed, allometric variables were shown to be most important in predicting RMR. Unfortunately, no suite of variables were shown to make reliable predictions, so the goal of estimating trophic impact from analyses of relationships between RMR and easily-attainable traits did not come to fruition.

One way in which case-studies are superior to lab studies when it comes to managing for aquatic invasive species (AIS) is they provide an idea of how organisms behave in field settings, under influences of various abiotic and biotic conditions and relative to native fish species. The work of Schulze *et al.* (2006) involved deliberately stocking Zander *Sander lucioperca* in a lake already containing Northern Pike *Esox lucius* and Eurasian Perch *Perca fluviatilis*. Caution must be used when deliberately stocking non-native species. The recipient ecosystem must be well contained, with no inflow or outflow, to prevent escape of species. One simply needs to examine the

example of Asian carp in North America to understand how easily some species can spread and proliferate (Koel *et al.* 2000). Case-studies provide a good alternative to deliberately stocking non-native species, as North America's long history of fish species introductions provide opportunities to examine interactions of invasive and native fish without the risks or time commitments of deliberate stocking. However, it is often difficult to find case-studies documenting all the required material needed to assess trophic impact though bioenergetic analyses, such as water temperature, prey proportions of both invasive and native fish species, and amount of diet overlap between the two groups including duration of diet overlap throughout the year.

Through analyses of some case-studies, the current research has examined how an invasive species in one area may not be harmful in another. Consistent with invasive species not being harmful in all areas, fish species with high bioenergetic rates relative to other species in one environment may not have high bioenergetic rates relative to species in a different environment. This finding was specifically addressed in the case of Lake Trout *Salvelinus namaycush* in Hector Lake, Alberta (Donald and Alger 1993), compared to Lake Trout in Lake Michigan. In the first case, Lake Trout displaced Bull Trout *Salvelinus confluentus* in Hector Lake, whereas evidence provided by Stewart and Ibarra (1991) suggested higher trophic impact by Chinook Salmon *Oncorhynchus tshawytscha* over Lake Trout in Lake Michigan.

Even though the current research has demonstrated that in many cases, invasive fish species have higher bioenergetic rates than native fish species, resulting in higher trophic impact on recipient environments, other research has shown impacts can still be realized from introductions of species with lower bioenergetic rates than native species,

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as indicated by the aforementioned work of Schulze *et al.* (2006). In this case, Zander caused forage fish to move to littoral areas, allowing the trophic impact of native Northern Pike to increase through elevated food consumption rate (FCR). In addition, the FCR of Eurasian Perch had decreased from stocking of Zander, so although Zander had the lowest FCR of the three species, impacts on the ecosystem were still observed after its introduction. Since the authors suggested there was competition between Eurasian Perch and Zander, it is evident Zander had some trophic impact in the system. Although they were shown to not have FCRs as great as those of Eurasian Perch, the increased number of predators introduced to the system through stocking of Zander had put additional pressure on available resources. It is critical to understand even though introduced species may demonstrate lower bioenergetic rates than native species, competition may still exist and initiate trophic disturbances in recipient systems. Despite this finding, the basis for this thesis as a whole remains valid, as it is evident AIS with greater bioenergetic rates will have greater trophic impact than AIS with low rates and, therefore, should be of management priority.

A disadvantage to examining case-studies in AIS management is the dissimilarity that often exists between environments. An advantage to lab studies over-case studies is in their ability to control for various factors affecting bioenergetic rates (Brett 1962) such as temperature, salinity, and oxygen content of the water, thereby providing the potential to compare species on level playing fields. Yet even though these factors can be controlled, it is naïve to think the plethora of bioenergetic rate data available were all determined through studies standardized to the same procedures, where fish were fasted for the same durations, oxygen content was maintained at the same level, etc.

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Theoretically, RMR is a good proxy for trophic impact due to its strong link to FCR. Approximately 44% and 37% of energy allocation in carnivores and herbivores, respectfully, is used through respiration (Brett and Groves 1979). However, there is speculation as to how much importance inter-study variation (differences in fasting duration, water quality, etc.) had in influencing the RMR measures retrieved, as there were cases in which similar species demonstrated dissimilar RMRs. In addition, more information is needed regarding routine activity of species in field settings. Activity multipliers in fish species can vary under different conditions, making it difficult to provide general estimates of RMR. In one field setting, RMR may comprise less caloric expenditure than in another field setting. Although multiple species were used in the work of Clausen (1936), his research suggests higher RMR in fish that live in streams as opposed to calm water.

In the end, the current research was unable to correlate fish traits with RMRs. Chapter 2 of this thesis provided evidence of the contribution of trophic impact to overall impact by linking high bioenergetic rates to fish species that have caused declines in abundance, FCR, and/or growth in native fish species. Due to the difficult nature of finding studies providing sufficient information to undertake trophic impact comparisons, as was done in the current research, it was suggested researchers either document all information required to calculate bioenergetic rates of co-existing invasive and native fish species (described in Chapter 2), or they provide some evaluation of these rates (FCR, RMR, or growth rate). It was also noted that environment and its native biota must be taken into consideration in AIS management, as some species may be invasive in one area, but not cause harm in another. The importance of taking environmental

characteristics and native species traits into account when managing for AIS has been

suggested by other researchers (Angermeier 1995; Reynolds *et al.* 2005; Olden *et al.*

2006). Further, it is important to consider influences of prior anthropogenic changes in

recipient environments on both the native and introduced species, as introduced species

may be more adapted to athropogenically altered environments than native species

(Olden *et al.* 2006). As well, habitat and diet overlap between species should be studied

over the course of an entire growing season to gain more insight into the temporal

duration of overlap required to cause harm to native species. It is possible significant

effects can arise from overlap occurring only during critical life stages or seasons.

Finally, Chapter 2 recommended researchers remain cognizant that introduced species

with lower bioenergetic rates than native species may still cause harm.

Chapter 3 of this thesis suggested including thermal regime and gill morphometry

as traits analyzed for relationships with RMR. Gills are the main area of oxygen

exchange in fish, and gill morphometrics have been shown to differ between active and

sedentary fish (Hughes 1966), therefore providing justification as traits to use in work

dealing with fish species oxygen consumption rates. Data on thermal regime is easily

accessible, but gill morphometry is not as abundant as the other traits used in the current

research. As mentioned previously, it would also be beneficial for researchers to

collaborate in such a way as to enhance similarity of respirometry procedures and

environments, helping ensure RMRs can be compared on level playing fields. Routine

activity must also be examined more closely for individual species to gain better insight

into RMR in field settings. To incorporate the findings of Clark and Johnson (1999),

who showed inter-family variation in oxygen consumption is greater than intra-family

variation, future work should look to generalize RMRs across fish families. Fish traits should also be generalized correspondingly, choosing traits that not only discriminate RMR, but also discriminate between families, making it more likely traits will correlate to RMR in future analyses. In addition, researchers must be cognizant that trophic impact is only one measure of impact. Parker *et al.* (1999) suggested impact is comprised of three things: 1) the impact of a single individual from the invading species; 2) the range of the invading species; and 3) the abundance of the invading species. Finally, similar to Chapter 2, Chapter 3 of this thesis recommended environmental conditions and native species in the recipient community be analyzed when managing for AIS (Angermeier 1995; Reynolds *et al.* 2005; Olden *et al.* 2006).

Based on the recommendations made here, it is possible to develop tools to aid decision makers in understanding trophic impact threats of AIS prior to their arrival or once they have been detected, allowing managers to allocate resources appropriately. However, researchers must ask themselves not only if the payoff of overcoming the challenges discussed will be worth the effort required, but also if these challenges can be overcome within a reasonable timeframe and without distracting from proven AIS management strategies. Each year, AIS cost Canada and the United States upwards of $35 and $137 billion in management expenditures and economic losses from resource declines (Primentel *et al.* 2000; Dawson 2002; Colautti *et al.* 2006). Clearly there is a desire to improve upon current AIS management strategies. Essington *et al.* (2001) emphasized the need for inexpensive, efficient methods of predicting impact that make use of available life-history. This research has made a contribution to this need by

correlating high bioenergetic rates with AIS and providing evidence for relationships

between fish traits and trophic impact.

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APPENDICES

A1. Fish physiological parameter values for use in the Wisconsin Bioenergetics Model (Hanson *et al.* 1997), used in Chapter 2.

	Bull Trout *Salvelinus confluentus*	Lake Trout *Salvelinus namaycush*	Gizzard Shad *Dorosoma cepedianum*	Bighead Carp *Hypophthalmichthys nobilis*	Silver Carp *Hypophthalmichthys molitrix*	Bloater *Coregonus hoyi*	Alewife *Alosa pseudoharengus*
Source	Mesa *et al.* 2013	Stewart *et al.* 1983	Sebring 2002 (MSc)	Cooke and Hill 2010	Cooke and Hill 2010	Rudstam *et al.* 1994	Stewart and Binkowski 1986
Lab rates standard (s) or routine (r)	s	s	s	s	s	s	s
Food consumption equation	3	1	2	2	2	2	3
CA	0.1317	0.0589	0.8081	1.54	1.54	1.61	0.8464
CB	-0.1396	-0.307	-0.3	-0.287	-0.287	-0.538	-0.3
CQ	3	0.1225	2.1	2.5	2.5	3.53	3
CTO	15.8	-	25	26	29	16.8	16
CTM	17.5	-	32.4	38	43	26	18
CTL	21	-	-	-	-	-	25
CK1	0.06	-	-	-	-	-	0.17
CK4	0.38	-	-	-	-	-	0.01
Metabolic equation	1	1	2	1	1	1	1
RA	0.0009	0.00463	0.005	0.0053	0.0028	0.0018	0.00367
RB	-0.1266	-0.295	-0.21	-0.299	-0.239	-0.12	-0.2152
RQ	0.0833	0.059	2.1	0.048	0.076	0.047	0.0548
RTO	**0.4831	0.0232	32.4	**0.5307	**0.5307	0.025	0.03

RTM	-	0	35.4	-	-	0	0
RTL	0	11	-	-	-	0	9
RK1	1	18.27	-	1	1	7.23	22.08
RK4	0	0.05	-	0	0	0.25	-0.045
ACT	1	11.7	3.9	1	1	0	5.78
BACT	-	0.0405	-	-	-	0	0.149
SDA	0.172	0.172	0.175	0.1	0.1	0.17	0.175
Egestion / excretion equation	*2	*2	1	2	2	1	1
FA	0.212	0.212	0.16	0.212	0.212	0.25	0.16
FB	-0.222	-0.222	-	-0.222	-0.222	0	0
FG	0.631	0.631	-	0.631	0.631	0	0
UA	0.0314	0.0314	0.1	0.031	0.031	0.1	0.1
UB	0.58	0.58	-	0.58	0.58	0	0
UG	-0.299	-0.299	-	-0.299	-0.299	0	0
Predator energy density	-	-	5233	5442	5442	-	5233
Alpha 1	5322	5701	-	-	-	3952	-
Beta 1	5.09	3.0809	-	-	-	58.7	-
Cutoff	100	1472	-	-	-	155	-
Alpha 2	6140	9092	-	-	-	13050	-
Beta 2	0.367	0.7786	-	-	-	0.001	-

*equation 2 used as opposed to 3
**estimate
A1. sources of data:

Cooke, S. L., and W. R. Hill. 2010. Can filter-feeding Asian carp invade the Laurentian Great Lakes? A bioenergetic modelling exercise. Freshwater Biology 55:2138-2152.
Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetic 3.0. University of Wisconsin, Center for Limnology, WISCU-T-97–001, Madison.

Mesa, M. G., L. K. Weiland, H. E. Christiansen, S. T. Sauter, and D. A. Beauchamp. 2013. Development and evaluation of a bioenergetics model for bull trout. Transactions of the American Fisheries Society 142:41-49.

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Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, Salvelinus namaycush: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681-698.

A2. Fish routine metabolic rate physiological parameter values for use in the Wisconsin Bioenergetics Model (Hanson *et al.* 1997), used in Chapter 3. Values based on fits of data points are approximations. Also shown are data used to generate fits, including temperature and weight bounds used in source studies.

Fish common name	Fish taxonomic name	Source	Lab rates standard (s) or routine (r)	Metabolic equation	RA	RB	RQ	RTO	RTM	RTL	RK1	RK4	ACT	BACT	SDA
Alewife	*Alosa pseudoharengus*	Stewart & Binkowski 1986	s	1	0.0037	-0.215	0.0548	0.03	0	9	22.08	-0.045	5.78	0.149	0.175
Atlantic Herring	*Clupea harengus*	Rudstam 1989	s	1	0.0033	-0.227	0.0548	0.03	0	9	15	0.13	3.9	0.149	0.175
Bighead Carp	*Hypophthalmichthys nobilis*	Cooke & Hill 2010	s	1	0.0053	-0.299	0.048	**0.5307	0	0	1	0	1	0	0.1
Bloater	*Coregonus hoyi*	Rudstam *et al.* 1994	s	1	0.0018	-0.12	0.047	0.025	0	0	7.23	0.25	1	0	0.17
Bluegill	*Lepomis macrochirus*	Kitchell *et al.* 1974	r	2	0.0154	-0.2	2.1	36	40	-	-	-	1	-	0.172
Brook Trout	*Salvelinus fontinalis*	Hartman & Cox 2008	s	2	0.0132	-0.265	4.5	20.2	25	-	-	-	2.89	-	0.172
Brown Bullhead	*Ameiurus nebulosus*	Dr. Kyle Hartman, Personal Communication, 2014	s	1	0.0006	-0.3	0.0918	**0.1398	0	0	1	0	1	0	0.172

Brown Trout	*Salmo trutta*	Dietermann *et al.* 2004	s	1	0.0013	-0.269	0.0938	0.0234	0	25	1	0.13	9.7	0.0405	0.172
Bull Trout	*Salvelinus confluentus*	Mesa *et al.* 2013	s	1	0.0009	-0.127	0.0833	**1.0082	0	0	1	0	1	0	0.172
Burbot	*Lota lota*	Rudstam *et al.* 1995	s	2	0.008	-0.172	1.88	21	24	-	-	-	1.25	-	0.2
Chinook Salmon	*Oncorhynchus tshawytscha*	Stewart & Ibarra 1991	s	1	0.0026	-0.217	0.0682	0.0234	0	25	26.7	0.13	9.7	0.0405	0.172
Eurasian Perch	*Perca fluviatilus*	Karas & Thoresson 1992	s	2	0.035	-0.2	2.8	28	33	-	-	-	1.1	-	0.15
European Flounder	*Platichthys flesus*	Stevens *et al.* 2006	s	2	0.0178	-0.218	2.5	21	27	-	-	-	1.1	-	0.19
Fathead Minnow	*Pimephales promelas*	Duffy 1998	r	2	0.0096	-0.041	2.6	28	33	-	-	-	1	-	0.172
Flathead Catfish (T<10°C)	*Pylodictis olivaris*	Roell and Orth 1993	s	2	0.01	-0.36	2.1	35	38	-	-	-	1.025	-	0.17
Flathead Catfish (T≥10°C)	*Pylodictis olivaris*	Roell and Orth 1993	s	2	0.01	-0.36	2.1	35	38	-	-	-	1.15	-	0.17
Gizzard Shad	*Dorosoma cepedianum*	Sebring 2002	s	2	0.005	-0.21	2.1	32.4	35.4	-	-	-	3.9	-	0.175

Common Name	Scientific Name	Reference													
Humpback Chub	*Gila cypha*	Petersen & Paukert 2005	s	2	0.0049	-0.084	2.42	28.2	31.6	-	-	-	1.16	-	0.15
Lake Trout	*Salvelinus namaycush*	Stewart *et al.* 1983	s	1	0.0046	-0.295	0.059	0.0232	0	11	18.27	0.05	11.7	0.0405	0.172
Lake Whitefish	*Coregonus clupeaformis*	Madenjian *et al.* 2006	s	1	0.0009	-0.12	0.047	0.025	0	0	7.23	0.25	1	0	0.17
Largemouth Bass	*Micropterus salmoides*	Rice *et al.* 1983	s	1	0.0028	-0.355	0.0811	0.0196	0	0	1	0	1	0	0.163
Northern Pike	*Esox lucius*	Bevelhimer *et al.* 1985	s	1	0.0025	-0.18	0.055	0.1222	0	0	1	0	1	0	0.14
Northern Pikeminnow	*Ptychocheilus oregonensis*	Zorich 2004	s	1	0.0017	-0.285	0.105	0.0234	0	0	28	0	1	0	0.163
Northern Redbelly Dace	*Chrosomus eos*	He 1986	r	2	0.0148	-0.2	2.1	29	32	-	-	-	1	-	0.15
Pallid Sturgeon (T<25°C)	*Scaphirhynchus albus*	Chipps *et al.* 2010	s	2	0.017	-0.15	1.92	30	35	-	-	-	1	-	0.13
Pallid Sturgeon (T≥25°C)	*Scaphirhynchus albus*	Chipps *et al.* 2010	s	2	0.017	-0.15	1.92	30	35	-	-	-	1.5	-	0.13
Pink Salmon	*Oncorhynchus gorbuscha*	Beauchamp *et al.* 1989	s	1	0.0014	-0.209	0.086	0.0234	0	25	27.25	0.13	9.9	0.0405	0.172

Prickly Sculpin	*Cottus asper*	Moss 2001	s	1	0.0021	-0.124	0.0616	**0.1824	0	0	1	0	1	0	0.175
Rainbow Smelt	*Osmerus mordax*	Lantry & Stewart 1993	r	1	0.0027	-0.216	0.036	0	0	0	0	0	1	0	0.175
Rainbow Trout	*Oncorhynchus mykiss*	Railsback and Rose 1999	s	2	0.013	-0.217	2.2	22	26	-	-	-	1.3	-	0.172
Rock Bass (T<10°C)	*Ambloplites rupestris*	Roell & Orth 1993	s	2	0.0108	-0.2	2.1	33	37	-	-	-	1.025	-	0.17
Rock Bass (T≥10°C)	*Ambloplites rupestris*	Roell & Orth 1993	s	2	0.0108	-0.2	2.1	33	37	-	-	-	1.15	-	0.17
Round Goby	*Neogobius melanostomus*	Lee and Johnson 2005	r	1	0.0009	-0.157	0.061	0	0	0	0	0	0	0	0.175
Ruffe	*Gymnocephalus cernua*	Tarvainen *et al.* 2008	r	2	0.0052	-0.129	4.007	20	30	-	-	-	1	-	0.124
Sacramento Perch	*Archoplites interruptus*	Bliesner 2005	r	2	0.005	-0.007	3.59	22.3	31.8	-	-	-	1	-	0.172
Saugeye	*Sander vitreus X S. canadensis*	Zweifel *et al.* 2010	r	2	0.031	-0.376	2.4	28	35	-	-	-	1	-	0.23
Sea Lamprey	*Petromyzon marinus*	Kitchell & Breck 1980	s	2	0.004	-0.05	2.1	25	30	-	-	-	1.5	-	0.172

Silver Carp	*Hypophthalmichthys molitrix*	Cooke & Hill 2010	s	1	0.0028	-0.239	0.076	**0.5307	0		1	0	1	0	0.1
Smallmouth Bass (T<10°C)	*Micropterus dolomieui*	Roell & Orth 1993	s	2	0.0084	-0.355	2.1	33	38	-	-	-	1.05	-	0.17
Smallmouth Bass (T≥10°C)	*Micropterus dolomieui*	Roell & Orth 1993	s	2	0.0084	-0.355	2.1	33	38	-	-	-	1.3	-	0.17
Striped Bass	*Morone saxatilis*	Hartman and Brandt 1995	s	1	0.0028	-0.218	0.076	0.5002	0	0	1	0	1	0	0.172
Threespine Stickleback	*Gasterosteus aculeatus*	Rachel Hovel, Personal Communication, 2014	s	1	0.001	-0.54	0.0839	0.0234	0	0	1	0	1	0	0.172
Walleye	*Sander vitreus*	Kitchell *et al.* 1977	r	2	0.0108	-0.2	2.1	27	32	-	-	-	1	-	0.172
Western Carp Gudgeon	*Hypseleotris klunzingeri*	S. Meredith, MDFRC, 2006	s	1	0.001	-0.391	0.0506	0.6	0	25	0.4	-0.1	0.08	0.07	0.175
White Crappie	*Pomoxis annularis*	Zweifel 2000; Bajer *et al.* 2004	s	1	0.0237	-0.623	0.0237	**0.2629	0	0	1	0	1	0	0.16
Yellow Perch	*Perca flavescens*	Kitchell *et al.* 1977	r	2	0.0108	-0.2	2.1	28	33	-	-	-	1	-	0.172
Zander	*Sander lucioperca*	Keskinen *et al.* 2008	r	2	0.005	-0.025	1.866	30	35	-	-	-	1	-	0.178

*unclear whether lab study determined standard (s) or routine (r) rates
**estimate

A2. Continued.

Fish common name	Fish taxonomic name	Source	Lab rates standard (s) or routine (r)	Metabolic equation	RA	RA source	RB	RB source	RQ	RQ source
American Eel	*Anguilla rostrata*	fit of data points	s	2	0.009715	started at 0.008 (value for Burbot), but adjusted after approximating RQ	-0.172	value for Burbot	2.8907	approximated using temperature-dependent equation
Atlantic Salmon	*Salmo salar*	fit of data points	r	1	0.00143	value for Sockeye Salmon	-0.209	value for Sockeye Salmon	0.069748	approximated using temperature-dependent equation
Bitterling	*Rhodeus sericeus*	fit of data points	r	2	0.0052053	value approximated for Goldfish	-0.119057	value approximated for Goldfish	1.60093	approximated using temperature-dependent equation
Central Mudminnow	*Umbra limi*	fit of data points	*r	1	0.00094	value for Round Goby	-0.157	value for Round Goby	0.0868523	approximated using temperature-dependent equation

Common Name	Scientific Name	Method			Value	Description	Value	Description	Value	Description
Common Carp	*Cyprinus carpio*	fit of data points	s	2	0.006764	approximated using allometric equation	-0.19	approximated using allometric equation	2.127	approximated using temperature-dependent equation
Crucian Carp	*Carassius carassius*	fit of data points	r	2	0.006764	value approximated for Common Carp	-0.19	value approximated for Common Carp	2.6327	approximated using temperature-dependent equation
European Brook Lamprey	*Lampetra planeri*	fit of data points	s	2	0.00397	value for Sea Lamprey	-0.05	value for Sea Lamprey	2.4149	approximated using temperature-dependent equation
European Eel	*Anguilla anguilla*	fit of data points	s	2	0.008	value for Burbot	-0.172	value for Burbot	1.8796	approximated using temperature-dependent equation
Flathead Mullet	*Mugil cephalus*	fit of data points	r	1	0.00085	value for Lake Whitefish	-0.12	value for Lake Whitefish	0.06188	approximated using temperature-dependent equation

Goldfish	*Carrasius auratus*	fit of data points	s	2	0.0052053	approximated using allometric equation	-0.119057	approximated using allometric equation	2.5868	approximated using temperature-dependent equation
Grass Carp	*Ctenopharyngodon idella*	fit of data points	*r	2	0.006764	value approximated for Common Carp	-0.12596	value approximated for Common Carp	2.127	value approximated for Common Carp
Green Sunfish	*Lepomis cyanellus*	fit of data points	r	2	0.0108	value for Rock Bass	-0.2	value for Rock Bass	1.863	approximated using temperature-dependent equation
Japanese Eel	*Anguilla japonica*	fit of data points	s	2	0.008	value for Burbot	-0.172	value for Burbot	3.6774	approximated using temperature-dependent equation
Marbled Sculpin	*Cottus klamathensis*	fit of data points	r	1	0.0021	value for Prickly Sculpin	-0.124	value for Prickly Sculpin	0.04672	approximated using temperature-dependent equation

Common Name	Scientific Name									
Mississippi Paddlefish	*Polyodon spathula*	fit of data points	r	2	0.007451	approximated using allometric equation (used 30°C as RTO in allometric fit, as this fit the data better than RTO listed in this table)	-0.098	approximated using allometric equation and 30°C as RTO, as this value fit the data better than RTO listed in this table	2.2598	approximated using temperature-dependent equation
Northern Snakehead	*Channa argus*	fit of data points	s	2	0.01637	approximated using allometric equation	-0.199	approximated using allometric equation	2.88394	approximated using temperature-dependent equation
Pit Sculpin	*Cottus pitensis*	fit of data points	r	1	0.0021	value for Prickly Sculpin	-0.124	value for Prickly Sculpin	0.064197	approximated using temperature-dependent equation
Pumpkinseed	*Lepomis gibbosus*	fit of data points	r	2	0.009	value for Smallmouth Bass (Shuter and Post 1990)	-0.21	value for Smallmouth Bass (Shuter and Post 1990)	2.9804	approximated using temperature-dependent equation
River Lamprey	*Lampetra fluviatilis*	fit of data points	s	2	0.00397	value for Sea Lamprey	-0.05	value for Sea Lamprey	2.3292	approximated using temperature-dependent equation and RTO=25 (value for Sea Lamprey). RTO adjusted after RQ was estimated.

Rough Sculpin	*Cottus asperrimus*	fit of data points	r	1	0.0021	value for Prickly Sculpin	-0.124	value for Prickly Sculpin	0.0574	approximated using temperature-dependent equation
White Sturgeon	*Acipenser transmontanus*	fit of data points	s	2	0.017	value for Pallid Sturgeon	-0.15	value for Pallid Sturgeon	2.71441	approximated using temperature-dependent equation
White Sucker	*Catostomus commersonii*	fit of data points	s	1	0.00165	value for Northern Pikeminnow	-0.285	value for Northern Pikeminnow	0.091784	approximated using temperature-dependent equation
Yellow Bullhead	*Ameiurus natalis*	fit of data points	r	1	0.00057	value for Brown Bullhead	-0.3	value for Brown Bullhead	0.0988	approximated using temperature-dependent equation

*unclear whether lab study determined standard (s) or routine (r) rates
**estimate

Fish common name	Fish taxonomic name	RTO	RTO source	RTM	RTM source	RTL	RTL source	RK1	RK1 source	RK4	RK4 source	ACT	ACT source	BACT	BACT source	SDA
American Eel	*Anguilla rostrata*	29.5	calculated based on final temperature preferendum (Hasnain 2012) and Jobling 1981	32.5	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.5	value for Sea Lamprey	-	-	-
Atlantic Salmon	*Salmo salar*	**1.0082	based on ACTIVITY of Chinook Salmon (wanted same ACTIVITY value as Chinook Salmon at its weight at maturity and final temperature preferendum)	0	added 3°C to final temperature preferendum provided by Hasnain 2012 (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-
Bitterling	*Rhodeus sericeus*	31.7	Hasain 2012	34.7	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.7	estimate	-	-	-
Central Mudminnow	*Umbra limi*	**0	since Lee and Johnson (2005) had modelled Round Goby using routine rates	0	added 3°C to final temperature preferendum (calculated based on upper lethal incipient temperature (Hasnain 2012) and Jobling 1981) (Hanson *et al.* 1997)	0	-	0	-	0	-	0	-	0	-	-

Common name	Scientific name		Source		Source											
Common Carp	*Cyprinus carpio*	34.5	Hasain 2012	37.5	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.7	estimate	-	-	-
Crucian Carp	*Carassius carassius*	30	adjusted (post-fit) from 31.7 (Hasnain 2012)	34.7	added 3°C to RTO provided by Hasnain 2012 (Hanson *et al.* 1997)	-	-	-	-	-	-	1.7	estimate	-	-	-
European Brook Lamprey	*Lampetra planeri*	25	value for Sea Lamprey	30	value for Sea Lamprey	-	-	-	-	-	-	1.5	value for Sea Lamprey	-	-	-
European Eel	*Anguilla anguilla*	29.6	calculated based on final temperature preferendum (used value for American Eel (Hasnain 2012)) and Jobling 1981	32.6	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.5	value for Sea Lamprey	-	-	-
Flathead Mullet	*Mugil cephalus*	**0.6932	wanted ACTIVITY=2	0	added 3°C to final temperature preferendum (Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)) (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-

Goldfish	*Carrasius auratus*	34.9	Hasnain 2012	37.9	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.7	estimate	-	-	-
Grass Carp	*Ctenopharyngodon idella*	32.4	Hasnain 2012	35.4	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.7	estimate	-	-	-
Green Sunfish	*Lepomis cyanellus*	40	Hasnain 2012	43	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.3	value for Smallmouth Bass	-	-	-
Japanese Eel	*Anguilla japonica*	29.6	calculated based on final temperature preferendum (used value for American Eel (Hasnain 2012)) and Jobling 1981	32.6	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.5	value for Sea Lamprey	-	-	-
Marbled Sculpin	*Cottus klamathensis*	**0.1824	wanted ACTIVITY=1.2 (Lee and Johnson (2005) suggest the value of 1.4 provided by Skazkina and Kostyuchenko (1968) is too high for gobies. As such, the current research deemed it too high for sculpins)	0	added 3°C to final temperature preferendum (Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)) (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-

Common Name	Scientific Name															
Mississippi Paddlefish	*Polyodon spathula*	28.3	calculated based on final temperature preferendum (used upper limit of temperature range (FishBase) and Jobling 1981	31.3	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.5	value for Pallid Sturgeon	-	-	-
Northern Snakehead	*Channa argus*	35	value for Striped Snakehead Channa striatus (Qin *et al.* 1997)	38	value for Striped Snakehead Channa striatus (Qin *et al.* 1997)	-	-	-	-	-	-	2	value for Striped Snakehead Channa striatus (Qin *et al.* 1997)	-	-	-
Pit Sculpin	*Cottus pitensis*	**0.1824	wanted ACTIVITY=1.2 (Lee and Johnson (2005) suggest the value of 1.4 provided by Skazkina and Kostyuchenko (1968) is too high for gobies. As such, the current research deemed it too high for sculpins)	0	added 3°C to final temperature preferendum (Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)) (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-
Pumpkinseed	*Lepomis gibbosus*	31.7	Hasnain 2012	34.7	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.3	value for Smallmouth Bass	-	-	-
River Lamprey	*Lampetra fluviatilis*	23	adjusted (post-fit) from value for Sea Lamprey	30	value for Sea Lamprey	-	-	-	-	-	-	1.5	value for Sea Lamprey	-	-	-

Common Name	Scientific Name		Notes		Notes											
Rough Sculpin	*Cottus asperrimus*	**0.1824	wanted ACTIVITY=1.2 (Lee and Johnson (2005) suggest the value of 1.4 provided by Skazkina and Kostyuchenko (1968) is too high for gobies. As such, the current research deemed it too high for sculpins)	0	added 3°C to final temperature preferendum (Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)) (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-
White Sturgeon	*Acipenser transmontanus*	30.6	calculated based on final temperature preferendum (calculated based on optimal growth temperature (Hasnain 2012) and Jobling 1981) and Jobling 1981	33.6	added 3°C to RTO (Hanson *et al.* 1997)	-	-	-	-	-	-	1.5	value for Pallid Sturgeon	-	-	-
White Sucker	*Catostomus commersonii*	**0.4055	based on Northern Pikeminnow (wanted slightly lower ACTIVITY due to more demersal habitat preference of White Sucker)	0	added 3°C to final temperature preferendum provided by Hasnain 2012 (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-
Yellow Bullhead	*Ameiurus natalis*	**0.1398	wanted ACTIVITY similar to that of Flathead Catfish	0	added 3°C to final temperature preferendum provided by Hasnain 2012 (Hanson *et al.* 1997)	0	-	1	-	0	-	1	-	0	-	-

*unclear whether lab study determined standard (s) or routine (r) rates

**estimate

A2. Continued.

Fish common name	Source of data points	Original units	Conversion factor	Equation	Temperature bounds (°C)	Temperature tested at in study (°C)	Weight bounds (g)	Weight tested at in study (g)	Metabolic rate (original units)	Metabolic rate (g $O_2 \cdot g$ fish$^{-1} \cdot$ day^{-1})	Activity multiplier	Routine metabolic rate (g $O_2 \cdot g$ fish$^{-1} \cdot$ day^{-1})	Notes	Lab rates standard (s) or routine (r)
American Eel	Degani and Lee-gallagher 1985	mg $O_2 \cdot$hr^{-1}	/1000/weight*24	ln(m)=ln(0.15)+0.57ln(w)	15 exactly	15	0.77-6.77	6	0.416522	0.001666	1.5	0.002499	-	s
American Eel	Degani and Lee-gallagher 1985	mg $O_2 \cdot$hr^{-1}	/1000/weight*24	ln(m)=ln(0.32)+0.52ln(w)	20 exactly	20	0.77-6.77	6	0.812435	0.00325	1.5	0.004875	-	s
American Eel	Degani and Lee-gallagher 1985	mg $O_2 \cdot$hr^{-1}	/1000/weight*24	ln(m)=ln(0.55)+0.57ln(w)	25 exactly	25	0.77-6.77	6	1.527246	0.006109	1.5	0.009163	-	s
Bitterling	FishBase	mg $O_2 \cdot$kg fish$^{-1} \cdot$hr^{-1}	/1000/1000*24	-	-	12	-	3	183	0.004392	-	0.004392	-	r
Bitterling	FishBase	mg $O_2 \cdot$kg fish$^{-1} \cdot$hr^{-1}	/1000/1000*24	-	-	14	-	3	193	0.004632	-	0.004632	-	r
Bitterling	FishBase	mg $O_2 \cdot$kg fish$^{-1} \cdot$hr^{-1}	/1000/1000*24	-	-	24	-	3	239	0.005736	-	0.005736	-	r
Central Mudminnow	Currie *et al.* 2010	umol $O_2 \cdot$g fish$^{-1} \cdot$hr^{-1}	/1000000*31.998*24	-	-	15	-	4.3	3.12	0.002396	-	0.002396	-	*r
Central Mudminnow	Currie *et al.* 2010	umol $O_2 \cdot$g fish$^{-1} \cdot$hr^{-1}	/1000000*31.998*24	-	-	19	-	4.3	5.17	0.00397	-	0.00397	-	*r
Central Mudminnow	Currie *et al.* 2010	umol $O_2 \cdot$g fish$^{-1} \cdot$hr^{-1}	/1000000*31.998*24	-	-	24	-	4.3	7.73	0.005936	-	0.005936	-	*r
Central Mudminnow	Currie *et al.* 2010	umol $O_2 \cdot$g fish$^{-1} \cdot$hr^{-1}	/1000000*31.998*24	-	-	28	-	4.3	10.52	0.008079	-	0.008079	-	*r
Central Mudminnow	Currie *et al.* 2010	umol $O_2 \cdot$g fish$^{-1} \cdot$hr^{-1}	/1000000*31.998*24	-	-	31	-	4.3	14.84	0.011396	-	0.011396	-	*r
Common Carp	Beamish 1964	mg $O_2 \cdot$hr^{-1}	/1000/weight*24	log(m)=-1.735+0.983log(w)	10 exactly	10	59-480	400	6.650051	0.000399	1.7	0.000678	-	s

Common Carp	Beamish 1964	mg O$_2$•hr^{-1}	/1000/weight*24	log(m)=-1.137+0.909log(w)	20 exactly	20	45-440	400	16.91502	0.001015	1.7	0.001725	-	s
Common Carp	Beamish 1964	mg O$_2$•hr^{-1}	/1000/weight*24	log(m)=-0.733+0.876log(w)	30 exactly	30	30-425	400	35.18881	0.002111	1.7	0.003589	-	s
Common Carp	Beamish 1964	mg O$_2$•hr^{-1}	/1000/weight*24	Log(m)=-0.550+0.810log(w)	35 exactly	35	50-400	400	36.11342	0.002167	1.7	0.003684	-	s
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	5	-	12.5	10	0.00024	-	0.00024	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	12.5	33	0.000792	-	0.000792	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	12.5	68	0.001632	-	0.001632	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	12.5	79	0.001896	-	0.001896	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	12.5	81	0.001944	-	0.001944	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	12.5	162	0.003888	-	0.003888	-	r
Crucian Carp	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	25	-	12.5	236	0.005664	-	0.005664	-	r
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	5.3	-	2.79	13	0.000312	1.5	0.000468	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	5.7	-	2.79	30	0.00072	1.5	0.00108	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	29	0.000696	1.5	0.001044	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	31	0.000744	1.5	0.001116	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	36	0.000864	1.5	0.001296	-	s

European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	41	0.000984	1.5	0.001476	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	45	0.00108	1.5	0.00162	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	55	0.00132	1.5	0.00198	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	62	0.001488	1.5	0.002232	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	71	0.001704	1.5	0.002556	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	72	0.001728	1.5	0.002592	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	82	0.001968	1.5	0.002952	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	2.79	101	0.002424	1.5	0.003636	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10.3	-	2.79	28	0.000672	1.5	0.001008	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10.6	-	2.79	69	0.001656	1.5	0.002484	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15.2	-	2.79	60	0.00144	1.5	0.00216	-	s
European Brook Lamprey	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15.6	-	2.79	103	0.002472	1.5	0.003708	-	s
European Eel	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	13	-	40	69	0.001656	1.5	0.002484	-	s
European Eel	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	17	-	40	126	0.003024	1.5	0.004536	-	s
Flathead Mullet	Marais 1978	mg O$_2$•hr^{-1}	/1000/weight*24	m=0.171*w^0.8485	13 exactly	13	5.7-15.4	13	1.507221	0.002783	-	0.002783	slight salinity	r

Flathead Mullet	Marais 1978	mg O$_2$•hr^{-1}	/1000/weight*24	m=0.254*w^0.8485	18 exactly	18	10.5-13.0	13	2.238797	0.004133	-	0.004133	slight salinity	r
Flathead Mullet	Marais 1978	mg O$_2$•hr^{-1}	/1000/weight*24	m=0.469*w^0.8485	28 exactly	28	7.7-24.6	13	4.133841	0.007632	-	0.007632	slight salinity	r
Flathead Mullet	Marais 1978	mg O$_2$•hr^{-1}	/1000/weight*24	m=0.566*w^0.8485	33 exactly	33	10.7-33.4	13	4.988815	0.00921	-	0.00921	slight salinity	r
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	100	16	0.000384	1.7	0.000653	-	s
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	12	-	100	43	0.001032	1.7	0.001754	-	s
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	100	30	0.00072	1.7	0.001224	-	s
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	30	-	100	72	0.001728	1.7	0.002938	-	s
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	32	-	100	149	0.003576	1.7	0.006079	-	s
Goldfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	35	-	100	127	0.003048	1.7	0.005182	-	s
Grass Carp	Zhao et al. 2011	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	265 exactly	265	40	0.00096	-	0.00096	-	*r
Grass Carp	Zhao et al. 2011	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	265 exactly	265	90	0.00216	-	0.00216	-	*r
Grass Carp	Zhao et al. 2011	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	265 exactly	265	145	0.00348	-	0.00348	-	*r
Grass Carp	Zhao et al. 2011	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	25	265 exactly	265	190	0.00456	-	0.00456	-	*r
Grass Carp	Zhao et al. 2011	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	30	265 exactly	265	210	0.00504	-	0.00504	-	*r
Green Sunfish	FishBase	mg O$_2$•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	10	130	0.00312	-	0.00312	-	r

Species	Source	Units	Conversion											
Green Sunfish	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	25	-	10	165	0.00396	-	0.00396	-	r
Green Sunfish	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	35	-	10	364	0.008736	-	0.008736	-	r
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	14.5	-	325	20	0.00048	1.5	0.00072	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	13	-	325	21	0.000504	1.5	0.000756	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	14.5	-	325	22	0.000528	1.5	0.000792	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	325	26	0.000624	1.5	0.000936	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	14.5	-	325	29	0.000696	1.5	0.001044	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	325	31	0.000744	1.5	0.001116	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	18.5	-	325	31	0.000744	1.5	0.001116	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	19	-	325	33	0.000792	1.5	0.001188	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	17	-	325	36	0.000864	1.5	0.001296	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	16	-	325	36	0.000864	1.5	0.001296	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	18	-	325	37	0.000888	1.5	0.001332	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	325	37	0.000888	1.5	0.001332	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	18	-	325	41	0.000984	1.5	0.001476	-	s

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Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	19.5	-	325	41	0.000984	1.5	0.001476	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	19.5	-	325	42	0.001008	1.5	0.001512	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	19	-	325	42	0.001008	1.5	0.001512	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	17	-	325	42	0.001008	1.5	0.001512	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	325	44	0.001056	1.5	0.001584	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	325	45	0.00108	1.5	0.00162	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	19	-	325	52	0.001248	1.5	0.001872	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	325	58	0.001392	1.5	0.002088	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	325	60	0.00144	1.5	0.00216	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	25	-	325	74	0.001776	1.5	0.002664	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	24	-	325	83	0.001992	1.5	0.002988	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	29	-	325	108	0.002592	1.5	0.003888	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	26	-	325	115	0.00276	1.5	0.00414	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	27.5	-	325	117	0.002808	1.5	0.004212	-	s
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	30	-	325	126	0.003024	1.5	0.004536	-	s

Species	Source	Units	Conversion	Mass equation	Temp (given)	Temp	Weight range	Max weight	Value	Result	Multiplier	Final		Type
Japanese Eel	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	29	-	325	137	0.003288	1.5	0.004932	-	s
Marbled Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	10	-	5.62	0.7354	0.00314	-	0.00314	-	r
Marbled Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	15	-	5.62	0.5721	0.002443	-	0.002443	-	r
Marbled Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	20	-	5.62	1.3164	0.005622	-	0.005622	-	r
Marbled Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	25	-	5.62	1.617	0.006905	-	0.006905	-	r
Mississippi Paddlefish	Patterson *et al.* 2013	mg O_2•hr^{-1}	/1000/weight*24	m=80.41*(w/1000)^0.918	10 exactly	10	280-11330	11300	744.7938	0.001582	-	0.001582	-	r
Mississippi Paddlefish	Patterson *et al.* 2013	mg O_2•hr^{-1}	/1000/weight*24	m=133.12*(w/1000)^0.935	20 exactly	20	500-11340	11300	1284.907	0.002729	-	0.002729	-	r
Mississippi Paddlefish	Patterson *et al.* 2013	mg O_2•hr^{-1}	/1000/weight*24	m=236.65*(w/1000)^0.902	30 exactly	30	420-12650	11300	2108.547	0.004478	-	0.004478	-	r
Northern Snakehead	Liu *et al.* 2000	mg O_2•hr^{-1}	/1000/weight*24	ln(m)=-7.863+0.801ln(w)+2.104ln(t)	10-35	10-35	41.5-510.3	292	4.612264	0.000379	2	0.000758	-	s
Pit Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	10	-	5.01	0.8397	0.004023	-	0.004023	-	r
Pit Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	15	-	5.01	0.9064	0.004342	-	0.004342	-	r
Pit Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	20	-	5.01	1.9271	0.009232	-	0.009232	-	r
Pit Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	25	-	5.01	1.9956	0.00956	-	0.00956	-	r
Pumpkinseed	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	5	-	30	23	0.000552	-	0.000552	-	r
Pumpkinseed	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	30	49	0.001176	-	0.001176	-	r

Species	Source	Units	Formula											
Pumpkinseed	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	15	-	30	73	0.001752	-	0.001752	-	r
Pumpkinseed	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	20	-	30	86	0.002064	-	0.002064	-	r
Pumpkinseed	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	25	-	30	120	0.00288	-	0.00288	-	r
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	4.4	-	1.43	16	0.000384	1.5	0.000576	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	4.8	-	1.43	35	0.00084	1.5	0.00126	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	1.43	38	0.000912	1.5	0.001368	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	1.43	40	0.00096	1.5	0.00144	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	9.4	-	1.43	41	0.000984	1.5	0.001476	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	1.43	44	0.001056	1.5	0.001584	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	1.43	48	0.001152	1.5	0.001728	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	14.4	-	1.43	78	0.001872	1.5	0.002808	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	10	-	1.43	83	0.001992	1.5	0.002988	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	9.8	-	1.43	83	0.001992	1.5	0.002988	-	s
River Lamprey	FishBase	mg O_2•kg fish^{-1}•hr^{-1}	/1000/1000*24	-	-	14.7	-	1.43	140	0.00336	1.5	0.00504	-	s
Rough Sculpin	Brown 1989	mg O_2•hr^{-1}	/1000/weight*24	-	-	10	-	2.59	0.4109	0.003808	-	0.003808	-	r

Species	Source	Units	Formula	Equation	Temp exactly	Temperature	Weight range	Weight	Value	Value	Mult	Value		s/r
Rough Sculpin	Brown 1989	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	-	-	15	-	2.59	0.3332	0.003088	-	0.003088	-	r
Rough Sculpin	Brown 1989	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	-	-	20	-	2.59	0.8423	0.007805	-	0.007805	-	r
Rough Sculpin	Brown 1989	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	-	-	25	-	2.59	1.0506	0.009735	-	0.009735	-	r
White Sturgeon	FishBase	mg $O_2{\cdot}kg\ fish^{-1}{\cdot}hr^{-1}$	/1000/1000*24	-	-	10	-	900	43	0.001032	1.5	0.001548	-	s
White Sturgeon	FishBase	mg $O_2{\cdot}kg\ fish^{-1}{\cdot}hr^{-1}$	/1000/1000*24	-	-	15	-	900	78	0.001872	1.5	0.002808	-	s
White Sucker	Beamish 1964	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	log(m)=-1.460+0.994log(w)	10 exactly	10	30-200	170	5.715658	0.000807	1.5	0.00121	-	s
White Sucker	Beamish 1964	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	log(m)=-0.772+0.828log(w)	15 exactly	15	18-295	170	11.87987	0.001677	1.5	0.002516	-	s
White Sucker	Beamish 1964	mg $O_2{\cdot}hr^{-1}$	/1000/weight*24	log(m)=-0.497+0.770log(w)	20 exactly	20	23-172	170	16.61291	0.002345	1.5	0.003518	-	s
Yellow Bullhead	FishBase	mg $O_2{\cdot}kg\ fish^{-1}{\cdot}hr^{-1}$	/1000/1000*24	-	-	22	-	5	214	0.005136	-	0.005136	-	r
Yellow Bullhead	FishBase	mg $O_2{\cdot}kg\ fish^{-1}{\cdot}hr^{-1}$	/1000/1000*24	-	-	27	-	5	210	0.00504	-	0.00504	-	r

*unclear whether lab study determined standard (s) or routine (r) rates

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A3. Species included in Chapter 3, including indication of use (x) in each dataset (mt = main training set, v = validation set, s = subset, r1-10 = reduced sets).

Fish common name	Fish taxonomic name	Fish order	Fish family	Dataset included in												
				mt	v	s	r1	r2	r3	r4	r5	r6	r7	r8	r9	r10
Pallid Sturgeon	*Scaphirhynchus albus*	Acipenseriformes	Acipenseridae	x	-	x	-	x	x	x	x	x	x	-	x	x
White Sturgeon	*Acipenser transmontanus*	Acipenseriformes	Acipenseridae	x	-	x	x	x	-	x	x	x	-	x	x	x
American Eel	*Anguilla rostrata*	Anguilliformes	Anguillidae	x	-	-	x	x	x	x	-	x	x	x	x	-
European Eel	*Anguilla anguilla*	Anguilliformes	Anguillidae	x	-	-	x	x	x	-	x	-	x	x	x	x
Japanese Eel	*Anguilla japonica*	Anguilliformes	Anguillidae	x	-	-	x	-	x	x	x	x	-	x	x	x
White Sucker	*Catostomus commersonii*	Cypriniformes	Catostomidae	x	-	x	x	x	-	x	x	x	x	-	x	x
Bluegill	*Lepomis macrochirus*	Perciformes	Centrarchidae	x	-	x	-	x	x	x	x	-	x	x	x	x
Green Sunfish	*Lepomis cyanellus*	Perciformes	Centrarchidae	x	-	-	-	x	x	x	x	x	x	-	x	x
Largemouth Bass	*Micropterus salmoides*	Perciformes	Centrarchidae	x	-	x	-	x	x	x	x	x	x	-	x	x
Pumpkinseed	*Lepomis gibbosus*	Perciformes	Centrarchidae	-	x	x	-	-	-	-	-	-	-	-	-	-
Rock Bass	*Ambloplites rupestris*	Perciformes	Centrarchidae	x	-	-	x	x	x	-	x	x	x	x	x	-
Sacramento Perch	*Archoplites interruptus*	Perciformes	Centrarchidae	x	-	-	x	x	x	-	x	x	x	x	-	x
Smallmouth Bass	*Micropterus dolomieui*	Perciformes	Centrarchidae	x	-	x	x	x	x	-	x	-	x	x	x	x

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White Crappie	*Pomoxis annularis*	Perciformes	Centrarchidae	-	x	-	-	-	-	-	-	-	-	-	-	-
Northern Snakehead	*Channa argus*	Perciformes	Channidae	x	-	x	x	x	-	x	x	x	x	-	x	x
Alewife	*Alosa pseudoharengus*	Clupeiformes	Clupeidae	x	-	x	x	-	x	x	x	x	x	x	-	x
Atlantic Herring	*Clupea harengus*	Clupeiformes	Clupeidae	x	-	x	x	x	x	-	x	x	x	x	x	-
Gizzard Shad	*Dorosoma cepedianum*	Clupeiformes	Clupeidae	x	-	x	x	x	-	x	x	x	-	x	x	x
Marbled Sculpin	*Cottus klamathensis*	Scorpaeniformes	Cottidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Pit Sculpin	*Cottus pitensis*	Scorpaeniformes	Cottidae	x	-	x	x	x	x	-	x	-	x	x	x	x
Prickly Sculpin	*Cottus asper*	Scorpaeniformes	Cottidae	x	-	-	x	x	x	-	x	x	x	x	x	-
Rough Sculpin	*Cottus asperrimus*	Scorpaeniformes	Cottidae	x	-	x	-	x	x	x	x	x	x	-	x	x
Bighead Carp	*Hypophthalmichthys nobilis*	Cypriniformes	Cyprinidae	x	-	x	x	x	-	x	x	x	x	x	-	x
Bitterling	*Rhodeus sericeus*	Cypriniformes	Cyprinidae	x	-	x	-	x	x	x	x	-	x	x	x	x
Common Carp	*Cyprinus carpio*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	-	x	x	x	x	-	x
Crucian Carp	*Carassius carassius*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	x	-	-	x	x	x	x
Fathead Minnow	*Pimephales promelas*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Goldfish	*Carrasius auratus*	Cypriniformes	Cyprinidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Grass Carp	*Ctenopharyngodon idella*	Cypriniformes	Cyprinidae	-	x	x	-	-	-	-	-	-	-	-	-	-

Common Name	Scientific Name	Order	Family												
Humpback Chub	*Gila cypha*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Northern Pikeminnow	*Ptychocheilus oregonensis*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Northern Redbelly Dace	*Chrosomus eos*	Cypriniformes	Cyprinidae	x	-	x	x	x	x	x	-	-	x	x	x	x
Silver Carp	*Hypophthalmichthys molitrix*	Cypriniformes	Cyprinidae	x	-	x	x	x	-	x	x	x	x	x	-	x
Western Carp Gudgeon	*Hypseleotris klunzingeri*	Perciformes	Eleotridae	x	-	-	x	x	-	x	x	x	x	x	-	x
Northern Pike	*Esox lucius*	Esociformes	Esocidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Threespine Stickleback	*Gasterosteus aculeatus*	Gasterosteiformes	Gasterosteidae	x	-	x	x	x	x	-	x	x	x	x	-	x
Round Goby	*Neogobius melanostomus*	Perciformes	Gobidae	x	-	x	x	x	x	-	x	x	x	x	x	-
Brown Bullhead	*Ameiurus nebulosus*	Siluriformes	Ictaluridae	-	x	x	-	-	-	-	-	-	-	-	-	-
Flathead Catfish	*Pylodictis olivaris*	Siluriformes	Ictaluridae	x	-	-	-	x	x	x	x	x	x	-	x	x
Yellow Bullhead	*Ameiurus natalis*	Siluriformes	Ictaluridae	-	x	-	-	-	-	-	-	-	-	-	-	-
Burbot	*Lota lota*	Gadiformes	Lotidae	x	-	x	-	x	x	x	x	x	x	-	x	x
Striped Bass	*Morone saxatilis*	Perciformes	Moronidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Flathead Mullet	*Mugil cephalus*	Mugiliformes	Mugilidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Rainbow Smelt	*Osmerus mordax*	Osmeriformes	Osmeridae	x	-	x	x	-	x	x	x	x	-	x	x	x
Eurasian Perch	*Perca fluviatilis*	Perciformes	Percidae	x	-	x	x	x	-	x	x	x	-	x	x	x

Ruffe	*Gymnocephalus cernua*	Perciformes	Percidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Saugeye	*Sander vitreus X S. canadensis*	Perciformes	Percidae	x	-	x	x	-	x	x	x	x	x	x	-	x
Walleye	*Sander vitreus*	Perciformes	Percidae	x	-	x	x	x	-	x	x	x	x	x	-	x
Yellow Perch	*Perca flavescens*	Perciformes	Percidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Zander	*Sander lucioperca*	Perciformes	Percidae	x	-	x	-	x	x	x	x	-	x	x	x	x
European Brook Lamprey	*Lampetra planeri*	Petromyzontiformes	Petromyzontidae	x	-	-	x	x	x	-	x	x	x	x	-	x
River Lamprey	*Lampetra fluviatilis*	Petromyzontiformes	Petromyzontidae	x	-	-	x	x	x	-	x	-	x	x	x	x
Sea Lamprey	*Petromyzon marinus*	Petromyzontiformes	Petromyzontidae	x	-	-	x	x	-	x	x	x	x	-	x	x
European Flounder	*Platichthys flesus*	Pleuronectiformes	Pleuronectidae	x	-	x	x	-	x	x	x	x	-	x	x	x
Mississippi Paddlefish	*Polyodon spathula*	Acipenseriformes	Polyodontidae	x	-	x	x	x	-	x	x	x	x	-	x	x
Atlantic Salmon	*Salmo salar*	Salmoniformes	Salmonidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Bloater	*Coregonus hoyi*	Salmoniformes	Salmonidae	x	-	x	x	x	-	x	x	x	-	x	x	x
Brook Trout	*Salvelinus fontinalis*	Salmoniformes	Salmonidae	x	-	x	-	x	x	x	x	x	x	-	x	x
Brown Trout	*Salmo trutta*	Salmoniformes	Salmonidae	x	-	x	x	-	x	x	x	x	x	x	-	x
Bull Trout	*Salvelinus confluentus*	Salmoniformes	Salmonidae	x	-	-	-	x	x	x	x	-	x	x	x	x
Chinook Salmon	*Oncorhynchus tshawytscha*	Salmoniformes	Salmonidae	x	-	-	-	x	x	x	x	x	x	-	x	x

Lake Trout	*Salvelinus namaycush*	Salmoniformes	Salmonidae	x	-	x	x	-	x	x	x	x	x	x	-	x
Lake Whitefish	*Coregonus clupeaformis*	Salmoniformes	Salmonidae	x	-	x	x	x	x	x	-	x	x	x	x	-
Pink Salmon	*Oncorhynchus gorbuscha*	Salmoniformes	Salmonidae	x	-	-	x	x	x	x	-	-	x	x	x	x
Rainbow Trout	*Oncorhynchus mykiss*	Salmoniformes	Salmonidae	x	-	x	x	x	x	x	-	-	x	x	x	x
Central Mudminnow	*Umbra limi*	Esociformes	Umbridae	-	x	x	-	-	-	-	-	-	-	-	-	-

A4. Representation of North American, north-temperate ($\geq$ 40°N latitude) fish families in Chapter 3.

Fish family	Number of species in dataset	Number of species in North America existing ≥ 40°N latitude	Fish family	Number of species in dataset	Number of species in North America existing ≥ 40°N latitude
Acipenseridae	2	5	Hiodontidae	0	2
Amiidae	0	1	Ictaluridae	3	10
Anguillidae	3	1	Lepisosteidae	0	3
Atherinopsidae	0	1	Loricariidae	0	1
Catostomidae	1	19	Lotidae	1	1
Centrarchidae	8	12	Moronidae	1	3
Channidae	1	0	Mugilidae	1	1
Characidae	0	1	Osmeridae	1	6
Cichlidae	0	5	Percidae	6	16
Clupeidae	3	6	Percopsidae	0	1
Cottidae	4	10	Petromyzontidae	3	12
Cyprinidae	11	55	Pleuronectidae	1	3
Eleotridae	1	0	Polyodontidae	1	1
Embiotocidae	0	1	Salmonidae	10	23
Esocidae	1	5	Sciaenidae	0	1
Fundulidae	0	4	Syngnathidae	0	1
Gasterosteidae	1	4	Umbridae	1	2
Gobidae	1	2			

A5. Routine metabolic rate of each species included in Chapter 3. Rates were calculated using the approximate weight at maturity and final temperature preferendum of each species.

Fish common name	Fish taxonomic name	Weight at maturity (g)	*Weight at maturity source	Final temperature preferendum (°C)	Final temperature preferendum source	Routine metabolic rate (g O$_2$ • g fish^{-1} • d^{-1})
Alewife	*Alosa pseudoharengus*	23	Eakins 2015 (smallest value in "adult weight" range provided)	16.9	Hasnain 2012	0.0084
American Eel	*Anguilla rostrata*	20	Eakins 2015 (smallest value in "adult weight" range provided)	19.9	Hasnain 2012	0.0044
Atlantic Herring	*Clupea harengus*	133	length-weight conversion (FishBase) using length at maturity (Fishbase)	21.5	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0083
Atlantic Salmon	*Salmo salar*	1100	Eakins 2015 (smallest value in "adult weight" range provided)	15.3	Hasnain 2012	0.0026
Bighead Carp	*Hypophthalmichthys nobilis*	8962	length-weight conversion (FishBase) using length at maturity (Fishbase)	26	Cooke and Hill 2010	0.0021
Bitterling	*Rhodeus sericeus*	0.74	length-weight conversion (FishBase) using length at maturity (Fishbase)	23.1	value for family (Hasnain 2012)	0.0075
Bloater	*Coregonus hoyi*	60	Eakins 2015 (smallest value in "adult weight" range provided)	16.8	Rudstam *et al.* 1994	0.0040

Bluegill	*Lepomis macrochirus*	50	Eakins 2015 (smallest value in "adult weight" range provided)	27	Kitchell *et al.* 1974	0.0047
Brook Trout	*Salvelinus fontinalis*	160	length-weight conversion (FishBase) using length at maturity (Scott and Crossman 1973)	14.8	Hasnain 2012	0.0060
Brown Bullhead	*Ameiurus nebulosus*	90	Eakins 2015 (smallest value in "adult weight" range provided)	26	Dr. Kyle Hartman, personal communication, 2014	0.0018
Brown Trout	*Salmo trutta*	60	Eakins 2015 (smallest value in "adult weight" range provided)	15.7	Hasnain 2012	0.0039
Bull Trout	*Salvelinus confluentus*	3404	length-weight conversion (FishBase) using length at maturity (Fishbase)	12.6	value for family (Hasnain 2012)	0.0025
Burbot	*Lota lota*	400	Eakins 2015 (smallest value in "adult weight" range provided)	13.7	Rudstam et al. 1995	0.0028
Central Mudminnow	*Umbra limi*	1	Eakins 2015 (smallest value in "adult weight" range provided)	25.8	calculated based on upper lethal incipient temperature (Hasnain 2012) and Jobling 1981	0.0088
Chinook Salmon	*Oncorhynchus tshawytscha*	1300	Eakins 2015 (smallest value in "adult weight" range provided)	13.8	Hasnain 2012	0.0039
Common Carp	*Cyprinus carpio*	600	Eakins 2015 (smallest value in "adult weight" range provided)	27.7	Hasnain 2012	0.0023

Crucian Carp	*Carassius carassius*	29	length-weight conversion (FishBase) using length at maturity (Tarkan et al. 2009)	23.1	value for family (Hasnain 2012)	0.0041
Eurasian Perch	*Perca fluviatilus*	36	length-weight conversion (FishBase) using length at maturity (FishBase)	23	Karas & Thoresson 1992	0.0145
European Brook Lamprey	*Lampetra planeri*	58	calculated using length at maturity and ratio of Sea Lamprey length at maturity to weight at maturity	18	value for Sea Lamprey	0.0034
European Eel	*Anguilla anguilla*	423	length-weight conversion (FishBase) using length at maturity (FishBase)	19.9	value for American Eel (Hasnain 2012)	0.0030
European Flounder	*Platichthys flesus*	99	length-weight conversion (FishBase) using length at maturity (FishBase)	16.5	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0060
Fathead Minnow	*Pimephales promelas*	1	Eakins 2015 (smallest value in "adult weight" range provided)	24	Duffy 1998	0.0082
Flathead Catfish	*Pylodictis olivaris*	40	length-weight conversion (FishBase) using length at maturity (FishBase)	24.3	family value (Hasnain 2012)	0.0019
Flathead Mullet	*Mugil cephalus*	541	length-weight conversion (FishBase) using length at maturity (FishBase)	34.4	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0067
Gizzard Shad	*Dorosoma cepedianum*	110	Eakins 2015 (smallest value in "adult weight" range provided)	25	Sebring 2002	0.0054

Goldfish	*Carrasius auratus*	260	Eakins 2015 (smallest value in "adult weight" range provided)	27.4	Hasnain 2012	0.0030
Grass Carp	*Ctenopharyngodon idella*	1500	Eakins 2015 (smallest value in "adult weight" range provided)	27.1	Hasnain 2012	0.0038
Green Sunfish	*Lepomis cyanellus*	20	Eakins 2015 (smallest value in "adult weight" range provided)	25.4	Hasnain 2012	0.0042
Humpback Chub	*Gila cypha*	113	length-weight conversion (FishBase) using length at maturity (Valdez and Ryel 1995)	28.1	Petersen & Paukert 2005	0.0038
Japanese Eel	*Anguilla japonica*	269	length-weight conversion (FishBase) using length at maturity (Okamura et al. 2007 (minimum of length range of silver stage 1 (i.e. when maturity first occurs)))	19.9	value for American Eel (Hasnain 2012)	0.0018
Lake Trout	*Salvelinus namaycush*	400	Eakins 2015 (smallest value in "adult weight" range provided)	11.8	Hasnain 2012	0.0028
Lake Whitefish	*Coregonus clupeaformis*	500	Eakins 2015 (smallest value in "adult weight" range provided)	16.8	Madenjian *et al.* 2006	0.0021
Largemouth Bass	*Micropterus salmoides*	400	Eakins 2015 (smallest value in "adult weight" range provided)	27.5	Rice *et al.* 1983	0.0032
Marbled Sculpin	*Cottus klamathensis*	2.58	length-weight conversion (FishBase) using length at maturity (Santos et al. 2013)	13.3	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0042

Common Name	Scientific Name	Value	Length/Weight Source	Temp	Temperature Source	Value
Mississippi Paddlefish	*Polyodon spathula*	12913	length-weight conversion (FishBase) using length at maturity (Adams 1942 (length of smallest spawning fish))	18	FishBase (upper limit of temperature range provided)	0.0026
Northern Pike	*Esox lucius*	600	Eakins 2015 (smallest value in "adult weight" range provided)	24	Bevelhimer *et al.* 1985	0.0033
Northern Pikeminnow	*Ptychocheilus oregonensis*	385	length-weight conversion (FishBase) using length at maturity (Scott and Crossman 1973)	23.1	family value (Hasnain 2012)	0.0066
Northern Redbelly Dace	*Chrosomus eos*	0.3	Eakins 2015 (smallest value in "adult weight" range provided)	26	He 1986	0.0175
Northern Snakehead	*Channa argus*	292	length-weight conversion (FishBase) using length at maturity (USGS 2012 (median of range provided))	30	value for Striped Snakehead *Channa striatus* (Qin et al. 1997)	0.0081
Pallid Sturgeon	*Scaphirhynchus albus*	654	length-weight conversion (FishBase) using length at maturity (FishBase)	28	Chipps *et al.* 2010	0.0094
Pink Salmon	*Oncorhynchus gorbuscha*	360	Eakins 2015 (smallest value in "adult weight" range provided)	13	Hasnain 2012	0.0030
Pit Sculpin	*Cottus pitensis*	1.51	length-weight conversion (FishBase) using length at maturity (Daniels 1987 (says they reach about 35% of maximum length in their first growing season; since maturity occurs at age 1 (California Fish Website 2015), the current research calculated 35% of max length))	13.3	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0056
Prickly Sculpin	*Cottus asper*	2.73	length-weight conversion (FishBase) using length at maturity (Rickard 1980)	13.3	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0050

Pumpkinseed	*Lepomis gibbosus*	40	Eakins 2015 (smallest value in "adult weight" range provided)	27.7	Hasnain 2012	0.0044
Rainbow Smelt	*Osmerus mordax*	10	Eakins 2015 (smallest value in "adult weight" range provided)	11.2	Hasnain 2012	0.0025
Rainbow Trout	*Oncorhynchus mykiss*	50	Eakins 2015 (smallest value in "adult weight" range provided)	15.5	Hasnain 2012	0.0055
River Lamprey	*Lampetra fluviatilis*	37	length-weight conversion (FishBase) using length at maturity (FishBase)	18	value for Sea Lamprey	0.0041
Rock Bass	*Ambloplites rupestris*	60	Eakins 2015 (smallest value in "adult weight" range provided)	24.9	Hasnain 2012	0.0039
Rough Sculpin	*Cottus asperrimus*	1.15	length-weight conversion (FishBase) using length at maturity (California Fish Website 2015)	13.3	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0053
Round Goby	*Neogobius melanostomus*	6	Eakins 2015 (smallest value in "adult weight" range provided)	22	Cherry and Cairns 1982 (median of general mean final temperature preferundum range provided for family)	0.0027
Ruffe	*Gymnocephalus cernua*	18	Eakins 2015 (smallest value in "adult weight" range provided)	19	Tarvainen *et al.* 2008	0.0035
Sacramento Perch	*Archoplites interruptus*	482	length-weight conversion (FishBase) using length at maturity (Crain and Moyle 2011)	20	Bliesner 2005	0.0044

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Saugeye	*Sander vitreus X S. canadensis*	100	Eakins 2015 (smallest value in "adult weight" range provided)	25	Zweifel *et al.* 2010	0.0051
Sea Lamprey	*Petromyzon marinus*	70	Eakins 2015 (smallest value in "adult weight" range provided)	18	Kitchell and Breck 1980	0.0036
Silver Carp	*Hypophthalmichthys molitrix*	3767	length-weight conversion (FishBase) using length at maturity (FishBase)	29	Cooke and Hill 2010	0.0060
Smallmouth Bass	*Micropterus dolomieui*	200	Eakins 2015 (smallest value in "adult weight" range provided)	25	Hasnain 2012	0.0012
Striped Bass	*Morone saxatilis*	806	length-weight conversion (FishBase) using length at maturity (Scott and Crossman 1973)	18.7	calculated based on upper lethal incipent temperature (Hasnain 2012) and Jobling 1981	0.0044
Threespine Stickleback	*Gasterosteus aculeatus*	1.1	Eakins 2015 (smallest value in "adult weight" range provided)	23	Hasnain 2012	0.0067
Walleye	*Sander vitreus*	200	Eakins 2015 (smallest value in "adult weight" range provided)	22	Kitchell *et al.* 1977	0.0032
Western Carp Gudgeon	*Hypseleotris klunzingeri*	1.21	length-weight conversion (FishBase) using length at maturity (FishBase life history tool)	25	S. Meredith, MDFRC, 2006	0.0043
White Crappie	*Pomoxis annularis*	50	Eakins 2015 (smallest value in "adult weight" range provided)	24	Zweifel 2000; Bajer *et al.* 2004	0.0048

White Sturgeon	*Acipenser transmontanus*	40202	length-weight conversion (FishBase) using length at maturity (FishBase)	21.5	calculated based on optimal growth temperature (Hasnain 2012) and Jobling 1981	0.0029
White Sucker	*Catostomus commersonii*	200	Eakins 2015 (smallest value in "adult weight" range provided)	23.4	Hasnain 2012	0.0047
Yellow Bullhead	*Ameiurus natalis*	80	Eakins 2015 (smallest value in "adult weight" range provided)	28.2	Hasnain 2012	0.0029
Yellow Perch	*Perca flavescens*	20	Eakins 2015 (smallest value in "adult weight" range provided)	23	Kitchell *et al.* 1977	0.0050
Zander	*Sander lucioperca*	550	length-weight conversion (FishBase) using length at maturity (FishBase)	24	Keskinen *et al.* 2008	0.0036

*in the absense of length-weight regressions for species, regressions for similar species were used

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A6. Trait data for each species examined in Chapter 3. K = von Bertalanffy growth coefficient, TRL = trophic level, TG = trophic guild, AM = age at maturity, ST = swim type, MW = maximum weight, MTL = maximum total length, SL = standard length to total length ratio, FL = fork length to total length ratio, PA = pre-anal length to total length ratio, PD = pre-dorsal length to total length ratio, PPEL = pre-pelvic length to total length ratio, BD = body depth to total length ratio, HL = head length to total length ratio, ED = eye diameter to head length ratio, PO = pre-orbital length to head length ratio, CA = caudal fin aspect ratio, BS = body shape, MP = mouth position, HP = habitat preference, ML = maximum lifespan, MF = maximum fecundity.

Fish common name	Fish taxonomic name	K	K source	TRL	TRL source	TG	TG source	AM (years)	AM source
Alewife	*Alosa pseudoharengus*	0.5333	FishBase	3.5	FishBase	carnivore	FishBase	3	FishBase
American Eel	*Anguilla rostrata*	-	-	3.9	FishBase	carnivore	FishBase	5	FishBase
Atlantic Herring	*Clupea harengus*	0.3506	FishBase	4.5	FishBase	carnivore	FishBase	3	FishBase
Atlantic Salmon	*Salmo salar*	0.2625	FishBase	4.5	FishBase	carnivore	FishBase	5	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	0.178	FishBase	2.3	FishBase	omnivore	FishBase	5	FishBase
Bitterling	*Rhodeus sericeus*	0.535	FishBase	2.11	FishBase ("Ecology" section)	omnivore	FishBase	3	FishBase

Bloater	*Coregonus hoyi*	0.1767	FishBase	3.4	FishBase	carnivore	Scott and Crossman 1973	3	FishBase
Bluegill	*Lepomis macrochirus*	0.3567	FishBase	3.5	FishBase	carnivore	FishBase	3	Scott and Crossman 1973
Brook Trout	*Salvelinus fontinalis*	0.32	FishBase	3.3	FishBase	carnivore	FishBase	3	Scott and Crossman 1973
Brown Bullhead	*Ameiurus nebulosus*	0.47	FishBase	4.4	FishBase	omnivore	FishBase	3	FishBase
Brown Trout	*Salmo trutta*	0.2844	FishBase	3.6	FishBase	carnivore	FishBase	2	FishBase
Bull Trout	*Salvelinus confluentus*	-	-	3.1	FishBase	carnivore	Hammond 2004	6	Hammond 2004
Burbot	*Lota lota*	0.1271	FishBase	4	FishBase	carnivore	FishBase	5	FishBase
Central Mudminnow	*Umbra limi*	0.655	FishBase	4.4	FishBase	carnivore	FishBase	2	Scott and Crossman 1973
Chinook Salmon	*Oncorhynchus tshawytscha*	-	-	4.4	FishBase	carnivore	FishBase	4	FishBase
Common Carp	*Cyprinus carpio*	0.2789	FishBase	3.1	FishBase	omnivore	FishBase	4	Scott and Crossman 1973 (average of median of ranges given)

Crucian Carp	*Carassius carassius*	0.09	FishBase	3.11	FishBase ("Ecology" section)	omnivore	FishBase	3	IUCN 2015
Eurasian Perch	*Perca fluviatilus*	0.2803	FishBase	4.4	FishBase	omnivore	FishBase	3	FishBase
European Brook Lamprey	*Lampetra planeri*	0.16	FishBase	4.37	value for Sea Lamprey	carnivore	estimate	5	FishBase (average of medians of ranges given)
European Eel	*Anguilla anguilla*	0.1597	FishBase	3.6	FishBase	carnivore	FishBase	11	FishBase
European Flounder	*Platichthys flesus*	0.3707	FishBase	3.5	FishBase	omnivore	FishBase	4	FishBase
Fathead Minnow	*Pimephales promelas*	0.7367	FishBase	3	FishBase	herbivore	FishBase	2	FishBase
Flathead Catfish	*Pylodictis olivaris*	-	-	4.3	FishBase	carnivore	Texas Parks and Wildlife	5	Texas Parks and Wildlife
Flathead Mullet	*Mugil cephalus*	0.3124	FishBase	3	FishBase	omnivore	FishBase	4	FishBase
Gizzard Shad	*Dorosoma cepedianum*	0.48	FishBase	2.4	FishBase	herbivore	Scott and Crossman 1973	2	FishBase
Goldfish	*Carrasius auratus*	0.225	FishBase	2	FishBase	omnivore	FishBase	2	FishBase

Grass Carp	*Ctenopharyngodon idella*	0.133	FishBase	2	FishBase	omnivore	FishBase	5	FishBase
Green Sunfish	*Lepomis cyanellus*	-	-	3.49	FishBase ("Ecology" section)	carnivore	Scott and Crossman 1973	3	University of Michigan Critter Catalogue 2015
Humpback Chub	*Gila cypha*	0.1767	FishBase	3	FishBase ("Estimates of some properties based on models" section)	carnivore	Valdez and Ryel 1995	3	Valdez and Ryel 1995
Japanese Eel	*Anguilla japonica*	0.07	FishBase	3.55	FishBase ("Ecology" section)	carnivore	FishBase	9	IUCN 2015
Lake Trout	*Salvelinus namaycush*	0.123	FishBase	4.3	FishBase	carnivore	FishBase	9	FishBase
Lake Whitefish	*Coregonus clupeaformis*	0.181	FishBase	3.3	FishBase	carnivore	FishBase	6	Eakins 2015 (median of range given)
Largemouth Bass	*Micropterus salmoides*	0.2133	FishBase	4.5	FishBase	carnivore	FishBase	4	Scott and Crossman 1973
Marbled Sculpin	*Cottus klamathensis*	0.28	FishBase	3.1	value for Prickly Sculpin	carnivore	estimate (Pit Sculpin)	2	California Fish Website 2015
Mississippi Paddlefish	*Polyodon spathula*	0.2125	FishBase	3	FishBase	omnivore	FishBase	9	Minnesota DNR 2015
Northern Pike	*Esox lucius*	0.1761	FishBase	4.5	FishBase	carnivore	FishBase	3	FishBase

Northern Pikeminnow	*Ptychocheilus oregonensis*	0.145	FishBase	4.4	FishBase	omnivore	FishBase	6	Scott and Crossman 1973
Northern Redbelly Dace	*Chrosomus eos*	1.13	FishBase	3.1	FishBase	omnivore	FishBase	1	Montana Official State Website 2015
Northern Snakehead	*Channa argus*	0.135	FishBase	4.5	FishBase	carnivore	Mayo 2005	3	USGS 2012
Pallid Sturgeon	*Scaphirhynchus albus*	0.13	FishBase	3.88	FishBase ("Ecology" section)	carnivore	FishBase	12	US EPA 2007
Pink Salmon	*Oncorhynchus gorbuscha*	-	-	4.5	FishBase	carnivore	FishBase	2	FishBase
Pit Sculpin	*Cottus pitensis*	0.19	FishBase	3.1	value for Prickly Sculpin	carnivore	California Fish Website 2015	1	California Fish Website 2015
Prickly Sculpin	*Cottus asper*	-	-	3.1	FishBase	carnivore	FishBase	3	California Fish Website 2015
Pumpkinseed	*Lepomis gibbosus*	0.2	FishBase	4.5	FishBase	carnivore	FishBase	2	FishBase
Rainbow Smelt	*Osmerus mordax*	0.4517	FishBase	4	FishBase	carnivore	FishBase	3	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	0.5483	FishBase	4.5	FishBase	carnivore	FishBase	4	Scott and Crossman 1973

Common Name	Scientific Name	Value	Source	Trophic Level	Source	Diet	Source	Value	Source
River Lamprey	*Lampetra fluviatilis*	-	-	4.5	FishBase ("Ecology" section)	carnivore	FishBase	6	FishBase (average of medians of ranges given)
Rock Bass	*Ambloplites rupestris*	-	-	3.7	FishBase	carnivore	FishBase	3	FishBase
Rough Sculpin	*Cottus asperrimus*	0.18	FishBase	3.1	value for Prickly Sculpin	carnivore	California Fish Website 2015	2	California Fish Website 2015
Round Goby	*Neogobius melanostomus*	0.5186	FishBase	3.9	FishBase	carnivore	FishBase	3	FishBase (average of medians of ranges given)
Ruffe	*Gymnocephalus cernua*	0.3641	FishBase	4	FishBase	carnivore	FishBase	2	FishBase
Sacramento Perch	*Archoplites interruptus*	-	-	3.7	value for Rock Bass	carnivore	California Fish Website 2015	3	California Fish Website 2015
Saugeye	*Sander vitreus X S. canadensis*	0.1767	FishBase	4.06	FishBase ("Ecology" section)	carnivore	Scott and Crossman 1973	4	Scott and Crossman 1973
Sea Lamprey	*Petromyzon marinus*	0.16	FishBase	4.37	FishBase ("Ecology" section)	carnivore	FishBase	7	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	0.21	FishBase	2	FishBase	omnivore	Indiana Government 2005	4	FishBase (average of medians of ranges given)
Smallmouth Bass	*Micropterus dolomieui*	0.176	FishBase	4.3	FishBase	carnivore	FishBase	5	Scott and Crossman 1973

Striped Bass	*Morone saxatilis*	0.19	FishBase	4.9	FishBase	carnivore	FishBase	5	NOAA Chesapeake Bay Office (average of medians of ranges given)
Threespine Stickleback	*Gasterosteus aculeatus*	2.3357	FishBase	3.8	FishBase	carnivore	FishBase	2	FishBase
Walleye	*Sander vitreus*	0.3063	FishBase	4.5	FishBase	carnivore	FishBase	4	Scott and Crossman 1973 (average of medians of ranges given)
Western Carp Gudgeon	*Hypseleotris klunzingeri*	-	-	3.4	FishBase	omnivore	FishBase	1	FishBase
White Crappie	*Pomoxis annularis*	-	-	4.4	FishBase	carnivore	FishBase	3	Scott and Crossman 1973
White Sturgeon	*Acipenser transmontanus*	0.0433	FishBase	3.4	FishBase	carnivore	Scott and Crossman 1973	23	Scott and Crossman 1973 (average of medians of ranges given for male and female)
White Sucker	*Catostomus commersonii*	0.14	FishBase	3.5	FishBase	carnivore	Scott and Crossman 1973	6	Scott and Crossman 1973 (give two ranges: 5-8 in general, but 3-4 in ontario, so took median of 3-8=5.5)
Yellow Bullhead	*Ameiurus natalis*	-	-	3.33	FishBase ("Ecology" section)	carnivore	Scott and Crossman 1973	3	Scott and Crossman 1973
Yellow Perch	*Perca flavescens*	0.2957	FishBase	4.1	FishBase	carnivore	FishBase	4	Scott and Crossman 1973 (average of male and female values)
Zander	*Sander lucioperca*	0.1309	FishBase	4.4	FishBase	carnivore	FishBase	4	FishBase

A6. Continued.

Fish common name	Fish taxonomic name	ST	ST source	MW (g)	MW source	MTL (mm)	MTL source
Alewife	*Alosa pseudoharengus*	carangiform/sub-carangiform	FishBase	200	FishBase	472	FishBase (converted from SL)
American Eel	*Anguilla rostrata*	anguilliform	FishBase	7300	FishBase	1520	FishBase
Atlantic Herring	*Clupea harengus*	carangiform/sub-carangiform	FishBase	1100	FishBase	536	FishBase (converted from SL)
Atlantic Salmon	*Salmo salar*	carangiform/sub-carangiform	FishBase	46800	FishBase	1500	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	carangiform/sub-carangiform	estimate (Common Carp)	40000	FishBase	1759	FishBase (converted from SL)
Bitterling	*Rhodeus sericeus*	carangiform/sub-carangiform	estimate (Goldfish)	25	Przybylski and Garcia-Berthou 2004 (using max length and equation given in paper)	110	FishBase
Bloater	*Coregonus hoyi*	carangiform/sub-carangiform	estimate (Salmon)	677	FishBase (length conversion)	370	FishBase
Bluegill	*Lepomis macrochirus*	labriform/diodontiform	estimate (Largemouth Bass)	2200	FishBase	410	FishBase

Brook Trout	*Salvelinus fontinalis*	carangiform/sub-carangiform	estimate (Trout)	9400	FishBase	947	FishBase (converted from SL)
Brown Bullhead	*Ameiurus nebulosus*	carangiform/sub-carangiform	FishBase	2700	FishBase	550	FishBase
Brown Trout	*Salmo trutta*	carangiform/sub-carangiform	FishBase	50000	FishBase	1573	FishBase (converted from SL)
Bull Trout	*Salvelinus confluentus*	carangiform/sub-carangiform	estimate (Trout)	14500	FishBase	1030	FishBase
Burbot	*Lota lota*	carangiform/sub-carangiform	FishBase	34000	FishBase	1520	FishBase
Central Mudminnow	*Umbra limi*	labriform/diodontiform	FishBase	42	FishBase (length conversion for Round Goby)	140	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	carangiform/sub-carangiform	FishBase	61400	FishBase	1500	FishBase
Common Carp	*Cyprinus carpio*	carangiform/sub-carangiform	FishBase	40100	FishBase	1332	FishBase (converted from SL)
Crucian Carp	*Carassius carassius*	carangiform/sub-carangiform	estimate (Common Carp)	3000	FishBase	640	FishBase
Eurasian Perch	*Perca fluviatilus*	carangiform/sub-carangiform	FishBase	4800	FishBase	697	FishBase (converted from SL)

European Brook Lamprey	*Lampetra planeri*	anguilliform	estimate (Sea Lamprey)	60	by comparing to River Lamprey	200	FishBase
European Eel	*Anguilla anguilla*	anguilliform	FishBase	6600	FishBase	1330	FishBase
European Flounder	*Platichthys flesus*	anguilliform	FishBase	14000	FishBase	600	FishBase
Fathead Minnow	*Pimephales promelas*	carangiform/sub-carangiform	estimate (Trout-like)	12	FishBase (length conversion)	101	FishBase
Flathead Catfish	*Pylodictis olivaris*	carangiform/sub-carangiform	estimate (Brown Bullhead)	55800	FishBase	1550	FishBase
Flathead Mullet	*Mugil cephalus*	carangiform/sub-carangiform	FishBase	20409	FishBase (length conversion)	1186	FishBase (converted from SL)
Gizzard Shad	*Dorosoma cepedianum*	carangiform/sub-carangiform	estimate (Alewife and Atlantic Herring)	2000	FishBase	635	FishBase (converted from fl)
Goldfish	*Carrasius auratus*	carangiform/sub-carangiform	FishBase	1223	FishBase (length conversion)	391	FishBase (converted from SL)
Grass Carp	*Ctenopharyngodon idella*	carangiform/sub-carangiform	estimate (Common Carp)	45000	FishBase	1500	FishBase
Green Sunfish	*Lepomis cyanellus*	labriform/diodontiform	estimate (Largemouth Bass)	960	FishBase	310	FishBase

Humpback Chub	*Gila cypha*	carangiform/sub-carangiform	estimate (Common Carp)	1165	Valdez and Ryel 1995	380	FishBase
Japanese Eel	*Anguilla japonica*	anguilliform	FishBase	1900	FishBase	1500	FishBase
Lake Trout	*Salvelinus namaycush*	carangiform/sub-carangiform	estimate (Salmon)	32700	FishBase	1500	FishBase
Lake Whitefish	*Coregonus clupeaformis*	carangiform/sub-carangiform	estimate	19000	FishBase	1000	FishBase
Largemouth Bass	*Micropterus salmoides*	labriform/diodontiform	FishBase	10100	FishBase	970	FishBase
Marbled Sculpin	*Cottus klamathensis*	labriform/diodontiform	estimate (Round Goby)	11	FishBase (length conversion for round goby)	90	FishBase
Mississippi Paddlefish	*Polyodon spathula*	carangiform/sub-carangiform	estimate (Sturgeon-like)	90700	FishBase	2210	FishBase
Northern Pike	*Esox lucius*	labriform/diodontiform	FishBase	28400	FishBase	1500	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	carangiform/sub-carangiform	estimate (Common Carp)	13000	FishBase Scott and Crossman 1973	630	FishBase
Northern Redbelly Dace	*Chrosomus eos*	carangiform/sub-carangiform	estimate (Common Carp)	2	Hatch 2002	80	FishBase

Northern Snakehead	*Channa argus*	carangiform/sub-carangiform	estimate (Burbot)	8000	FishBase	1000	FishBase
Pallid Sturgeon	*Scaphirhynchus albus*	carangiform/sub-carangiform	estimate	130000	FishBase	2000	FishBase
Pink Salmon	*Oncorhynchus gorbuscha*	carangiform/sub-carangiform	FishBase	6800	FishBase	760	FishBase
Pit Sculpin	*Cottus pitensis*	labriform/diodontiform	estimate (Round Goby)	34	FishBase (length conversion for Round Goby)	130	FishBase
Prickly Sculpin	*Cottus asper*	labriform/diodontiform	estimate (Round Goby)	412	FishBase (length conversion for Round Goby)	300	FishBase
Pumpkinseed	*Lepomis gibbosus*	labriform/diodontiform	estimate (Largemouth Bass)	630	FishBase	400	FishBase
Rainbow Smelt	*Osmerus mordax*	carangiform/sub-carangiform	estimate (Trout-like)	348	FishBase (length conversion)	356	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	carangiform/sub-carangiform	FishBase	25400	FishBase	1200	FishBase
River Lamprey	*Lampetra fluviatilis*	anguilliform	estimate (Sea Lamprey)	150	FishBase	500	FishBase
Rock Bass	*Ambloplites rupestris*	labriform/diodontiform	estimate (Largemouth Bass)	1400	FishBase	430	FishBase

Rough Sculpin	*Cottus asperrimus*	labriform/diodontiform	estimate (Round Goby)	14	FishBase (length conversion for Round Goby)	96	FishBase
Round Goby	*Neogobius melanostomus*	labriform/diodontiform	FishBase	228	FishBase	246	FishBase
Ruffe	*Gymnocephalus cernua*	carangiform/sub-carangiform	estimate (Yellow Perch)	400	FishBase	250	FishBase
Sacramento Perch	*Archoplites interruptus*	labriform/diodontiform	estimate (Largemouth Bass)	1400	FishBase	730	FishBase
Saugeye	*Sander vitreus X S. canadensis*	carangiform/sub-carangiform	estimate (Yellow Perch)	4000	FishBase	760	FishBase
Sea Lamprey	*Petromyzon marinus*	anguilliform	FishBase	2500	FishBase	1200	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	carangiform/sub-carangiform	estimate (Common Carp)	50000	FishBase	1050	FishBase
Smallmouth Bass	*Micropterus dolomieui*	labriform/diodontiform	estimate (Largemouth Bass)	5400	FishBase	690	FishBase
Striped Bass	*Morone saxatilis*	carangiform/sub-carangiform	FishBase	57000	FishBase	2000	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	labriform/diodontiform	FishBase	18	FishBase	110	FishBase

Walleye	*Sander vitreus*	carangiform/sub-carangiform	estimate (Yellow Perch)	11300	FishBase	1124	FishBase (converted from fl)
Western Carp Gudgeon	*Hypseleotris klunzingeri*	carangiform/sub-carangiform	estimate (Percid-like)	3	estimate based on max. length	65	FishBase
White Crappie	*Pomoxis annularis*	labriform/diodontiform	estimate (Largemouth Bass)	2400	FishBase	530	FishBase
White Sturgeon	*Acipenser transmontanus*	carangiform/sub-carangiform	estimate	816000	FishBase	6100	FishBase
White Sucker	*Catostomus commersonii*	carangiform/sub-carangiform	estimate	2900	FishBase	650	FishBase
Yellow Bullhead	*Ameiurus natalis*	carangiform/sub-carangiform	estimate (Brown Bullhead)	1900	FishBase	470	FishBase
Yellow Perch	*Perca flavescens*	carangiform/sub-carangiform	FishBase	1900	FishBase	500	FishBase
Zander	*Sander lucioperca*	carangiform/sub-carangiform	estimate (Yellow Perch)	20000	FishBase	1148	FishBase (converted from SL)

A6. Continued.

Fish common name	Fish taxonomic name	SL (%)	SL source	FL (%)	FL source	PA (%)	PA source	PD (%)	PD source
Alewife	*Alosa pseudoharengus*	84.8	FishBase	89.9	FishBase	62.6	FishBase	33.3	FishBase
American Eel	*Anguilla rostrata*	98.1	FishBase	100	FishBase	45.5	FishBase	34	FishBase
Atlantic Herring	*Clupea harengus*	84	FishBase	91.3	FishBase	63.8	FishBase	42.1	FishBase
Atlantic Salmon	*Salmo salar*	90.5	FishBase	95.6	FishBase	65.1	FishBase	38	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	83	FishBase	88.4	FishBase	53.5	FishBase	42.2	FishBase
Bitterling	*Rhodeus sericeus*	84.1	FishBase	91.2	FishBase	49.3	FishBase	42	FishBase
Bloater	*Coregonus hoyi*	87.7	FishBase	94	FishBase	67.2	FishBase	45.3	FishBase
Bluegill	*Lepomis macrochirus*	81.6	FishBase	95.4	FishBase	49.6	FishBase	26.4	FishBase

Brook Trout	*Salvelinus fontinalis*	90.8	FishBase	98.8	FishBase	66.7	FishBase	42.1	FishBase
Brown Bullhead	*Ameiurus nebulosus*	85.5	FishBase	99	FishBase	52.6	FishBase	29.7	FishBase
Brown Trout	*Salmo trutta*	89	FishBase	97.5	FishBase	66.6	FishBase	40.7	FishBase
Bull Trout	*Salvelinus confluentus*	90.4	FishBase	97.6	FishBase	65.5	FishBase	43.3	FishBase
Burbot	*Lota lota*	92.1	FishBase	100	FishBase	48.2	FishBase	34.1	FishBase
Central Mudminnow	*Umbra limi*	83.2	FishBase	100	observation	55.4	FishBase	49	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	87.7	FishBase	96.7	FishBase	65.9	FishBase	42.7	FishBase
Common Carp	*Cyprinus carpio*	82.6	FishBase	89.9	FishBase	63.8	FishBase	38.1	FishBase
Crucian Carp	*Carassius carassius*	82.3	FishBase	90.4	FishBase	64.1	FishBase	37.2	FishBase
Eurasian Perch	*Perca fluviatilus*	86.1	FishBase	95.3	FishBase	57.5	FishBase	23.3	FishBase

European Brook Lamprey	*Lampetra planeri*	97.8	FishBase	100	FishBase	-	-	62.4	FishBase
European Eel	*Anguilla anguilla*	98.4	FishBase	100	FishBase	46.4	FishBase	34.1	FishBase
European Flounder	*Platichthys flesus*	84.6	FishBase	100	FishBase	31.5	FishBase	21.4	FishBase
Fathead Minnow	*Pimephales promelas*	83	FishBase	95.2	FishBase	55.6	FishBase	42.4	FishBase
Flathead Catfish	*Pylodictis olivaris*	82.4	FishBase	99.3	FishBase	62.3	FishBase	35.7	FishBase
Flathead Mullet	*Mugil cephalus*	84.3	FishBase	92.6	FishBase	58.8	FishBase	40.5	FishBase
Gizzard Shad	*Dorosoma cepedianum*	84.5	FishBase	89.8	FishBase	53.8	FishBase	38.9	FishBase
Goldfish	*Carrasius auratus*	81.8	FishBase	92.9	FishBase	59.9	FishBase	36.7	FishBase
Grass Carp	*Ctenopharyngodon idella*	81.2	FishBase	88.2	FishBase	60	FishBase	42	FishBase
Green Sunfish	*Lepomis cyanellus*	84.8	FishBase	98.8	FishBase	52.8	FishBase	32.3	FishBase

Humpback Chub	*Gila cypha*	79.9	FishBase	88.2	FishBase	49.8	FishBase	37.6	FishBase
Japanese Eel	*Anguilla japonica*	99.6	FishBase	100	FishBase	39.3	FishBase	29.2	FishBase
Lake Trout	*Salvelinus namaycush*	89.3	FishBase	93.2	FishBase	70.9	FishBase	45.9	FishBase
Lake Whitefish	*Coregonus clupeaformis*	85.2	FishBase	91.7	FishBase	66.1	FishBase	37.7	FishBase
Largemouth Bass	*Micropterus salmoides*	85.8	FishBase	96.8	FishBase	51.5	FishBase	30.3	FishBase
Marbled Sculpin	*Cottus klamathensis*	84.1	measured image	100	measured image	47.1	measured image	28.7	measured image
Mississippi Paddlefish	*Polyodon spathula*	89.7	FishBase	92.5	FishBase	71.4	FishBase	67.5	FishBase
Northern Pike	*Esox lucius*	86.1	FishBase	93.2	FishBase	64.5	FishBase	61.8	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	89	FishBase	95.1	FishBase	69.7	FishBase	56.1	FishBase
Northern Redbelly Dace	*Chrosomus eos*	82.8	FishBase	93.6	FishBase	51.1	FishBase	43.6	FishBase

Northern Snakehead	*Channa argus*	84.9	FishBase	100	FishBase	44.7	FishBase	30.1	FishBase
Pallid Sturgeon	*Scaphirhynchus albus*	99.3	measured image	92.3	measured image	66.2	measured image	62	measured image
Pink Salmon	*Oncorhynchus gorbuscha*	89.7	FishBase	97.3	FishBase	65.8	FishBase	43	FishBase
Pit Sculpin	*Cottus pitensis*	83.4	measured image	100	measured image	48.4	measured image	27.4	measured image
Prickly Sculpin	*Cottus asper*	84.4	FishBase	100	FishBase	46	FishBase	27.8	FishBase
Pumpkinseed	*Lepomis gibbosus*	80.8	FishBase	100	FishBase	51.6	FishBase	28.1	FishBase
Rainbow Smelt	*Osmerus mordax*	86.8	FishBase	94.1	FishBase	61.7	FishBase	43.4	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	89.8	FishBase	98.2	FishBase	68.6	FishBase	39.9	FishBase
River Lamprey	*Lampetra fluviatilis*	100	measured image	100	measured image	-	-	46	measured image
Rock Bass	*Ambloplites rupestris*	78.9	FishBase	100	FishBase	47.2	FishBase	31.2	FishBase

Rough Sculpin	*Cottus asperrimus*	84.2	measured image	100	measured image	44.7	measured image	27.6	measured image
Round Goby	*Neogobius melanostomus*	84.8	FishBase	100	FishBase	46.3	FishBase	25.1	FishBase
Ruffe	*Gymnocephalus cernua*	86.2	FishBase	97.1	FishBase	59.6	FishBase	26.2	FishBase
Sacramento Perch	*Archoplites interruptus*	83.1	FishBase	98.1	FishBase	46	FishBase	30.2	FishBase
Saugeye	*Sander vitreus X S. canadensis*	90.7	FishBase	98	FishBase	59.4	FishBase	27.5	FishBase
Sea Lamprey	*Petromyzon marinus*	96.2	FishBase	100	FishBase	-	-	55.8	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	85.3	FishBase	90.7	FishBase	59.1	FishBase	42.7	FishBase
Smallmouth Bass	*Micropterus dolomieui*	82.8	FishBase	96.5	FishBase	55.6	FishBase	32.6	FishBase
Striped Bass	*Morone saxatilis*	83	FishBase	92.2	FishBase	56.1	FishBase	29.7	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	89.2	FishBase	98.8	FishBase	64.2	FishBase	31.3	FishBase

Walleye	*Sander vitreus*	86.7	FishBase	95.2	FishBase	57.6	FishBase	24	FishBase
Western Carp Gudgeon	*Hypseleotris klunzingeri*	85.1	measured image	100	measured image	48.5	measured image	31.3	measured image
White Crappie	*Pomoxis annularis*	82.3	FishBase	96.8	FishBase	46.7	FishBase	39.8	FishBase
White Sturgeon	*Acipenser transmontanus*	98.7	measured image	88.7	measured image	68.7	measured image	62.7	measured image
White Sucker	*Catostomus commersonii*	85.8	FishBase	94.5	FishBase	65.7	FishBase	43.6	FishBase
Yellow Bullhead	*Ameiurus natalis*	85.7	FishBase	98.9	FishBase	49.6	FishBase	28.9	FishBase
Yellow Perch	*Perca flavescens*	84.6	FishBase	97.6	FishBase	61.1	FishBase	24.6	FishBase
Zander	*Sander lucioperca*	87.1	FishBase	93.6	FishBase	54.2	FishBase	26.3	FishBase

A6. Continued.

Fish common name	Fish taxonomic name	PPEL (%)	PPEL source	PPEC (%)	PPEC source	BD (%)	BD source	HL (%)	HL source
Alewife	*Alosa pseudoharengus*	38.6	FishBase	16.4	FishBase	28.3	FishBase	16.9	FishBase
American Eel	*Anguilla rostrata*	-	-	12.9	FishBase	6.8	FishBase	11.7	FishBase
Atlantic Herring	*Clupea harengus*	47.2	FishBase	20.6	FishBase	16.9	FishBase	20.9	FishBase
Atlantic Salmon	*Salmo salar*	47.3	FishBase	20.4	FishBase	18.6	FishBase	21.2	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	38.7	FishBase	27.1	FishBase	25.9	FishBase	30.2	FishBase
Bitterling	*Rhodeus sericeus*	36.2	FishBase	18.9	FishBase	29.6	FishBase	18.4	FishBase
Bloater	*Coregonus hoyi*	49.2	FishBase	18.8	FishBase	20.5	FishBase	21.2	FishBase
Bluegill	*Lepomis macrochirus*	29.8	FishBase	24.5	FishBase	40.5	FishBase	27.1	FishBase

Brook Trout	*Salvelinus fontinalis*	45.5	FishBase	18.6	FishBase	26.4	FishBase	19.5	FishBase
Brown Bullhead	*Ameiurus nebulosus*	38.9	FishBase	20.8	FishBase	20.8	FishBase	22.4	FishBase
Brown Trout	*Salmo trutta*	49	FishBase	20.3	FishBase	18.6	FishBase	20.3	FishBase
Bull Trout	*Salvelinus confluentus*	45.8	FishBase	22	FishBase	15.6	FishBase	19	FishBase
Burbot	*Lota lota*	15.8	FishBase	20.7	FishBase	12.6	FishBase	19.4	FishBase
Central Mudminnow	*Umbra limi*	45.3	FishBase	24.2	FishBase	17.4	FishBase	24.5	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	50.5	FishBase	22.8	FishBase	21.5	FishBase	22	FishBase
Common Carp	*Cyprinus carpio*	39.3	FishBase	21	FishBase	31.3	FishBase	22.3	FishBase
Crucian Carp	*Carassius carassius*	39.2	FishBase	20	FishBase	38.1	FishBase	20.2	FishBase
Eurasian Perch	*Perca fluviatilus*	27.4	FishBase	26.7	FishBase	27.3	FishBase	26.9	FishBase

European Brook Lamprey	*Lampetra planeri*	-	-	-	-	8	FishBase	21.7	FishBase
European Eel	*Anguilla anguilla*	-	-	13.9	FishBase	6	FishBase	12.9	FishBase
European Flounder	*Platichthys flesus*	19.8	FishBase	21.7	FishBase	37.9	FishBase	21.2	FishBase
Fathead Minnow	*Pimephales promelas*	43.4	FishBase	20.1	FishBase	18.3	FishBase	18.6	FishBase
Flathead Catfish	*Pylodictis olivaris*	48.1	FishBase	23.3	FishBase	19.4	FishBase	26.6	FishBase
Flathead Mullet	*Mugil cephalus*	29.5	FishBase	20.1	FishBase	19.9	FishBase	18.1	FishBase
Gizzard Shad	*Dorosoma cepedianum*	33.2	FishBase	17.2	FishBase	32.3	FishBase	18.2	FishBase
Goldfish	*Carrasius auratus*	37.6	FishBase	21.9	FishBase	27.9	FishBase	22.6	FishBase
Grass Carp	*Ctenopharyngodon idella*	42.5	FishBase	22	FishBase	23	FishBase	21.8	FishBase
Green Sunfish	*Lepomis cyanellus*	33.1	FishBase	31.1	FishBase	34.6	FishBase	33.1	FishBase

Humpback Chub	*Gila cypha*	34.9	FishBase	18	FishBase	22.4	FishBase	16.2	FishBase
Japanese Eel	*Anguilla japonica*	-	-	11.7	FishBase	5	FishBase	11.5	FishBase
Lake Trout	*Salvelinus namaycush*	53.2	FishBase	20.5	FishBase	19.1	FishBase	20.5	FishBase
Lake Whitefish	*Coregonus clupeaformis*	42.7	FishBase	15.1	FishBase	21.7	FishBase	14.6	FishBase
Largemouth Bass	*Micropterus salmoides*	24.2	FishBase	27.1	FishBase	28	FishBase	28.2	FishBase
Marbled Sculpin	*Cottus klamathensis*	25.5	measured image	24.2	measured image	21	measured image	26.1	measured image
Mississippi Paddlefish	*Polyodon spathula*	58.9	FishBase	40.4	FishBase	18.7	FishBase	49.7	FishBase
Northern Pike	*Esox lucius*	45	FishBase	22.1	FishBase	13.2	FishBase	24.3	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	57.4	FishBase	28.3	FishBase	23.3	FishBase	30	FishBase
Northern Redbelly Dace	*Chrosomus eos*	38.1	FishBase	18.6	FishBase	16.7	FishBase	18.3	FishBase

Northern Snakehead	*Channa argus*	31.6	FishBase	29.9	FishBase	12.7	FishBase	28.6	FishBase
Pallid Sturgeon	*Scaphirhynchus albus*	51.4	measured image	25.4	measured image	12.7	measured image	25.4	measured image
Pink Salmon	*Oncorhynchus gorbuscha*	50.1	FishBase	20	FishBase	22.8	FishBase	20.6	FishBase
Pit Sculpin	*Cottus pitensis*	23.6	measured image	21	measured image	20.4	measured image	25.5	measured image
Prickly Sculpin	*Cottus asper*	26	FishBase	21.6	FishBase	18.3	FishBase	26	FishBase
Pumpkinseed	*Lepomis gibbosus*	32.5	FishBase	26.7	FishBase	44.1	FishBase	30.9	FishBase
Rainbow Smelt	*Osmerus mordax*	44.6	FishBase	18.8	FishBase	12.9	FishBase	18.1	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	46.7	FishBase	20.5	FishBase	22.8	FishBase	21.6	FishBase
River Lamprey	*Lampetra fluviatilis*	-	-	-	-	6.8	measured image	21.7	measured image
Rock Bass	*Ambloplites rupestris*	29.8	FishBase	27.6	FishBase	33.3	FishBase	28	FishBase

Rough Sculpin	*Cottus asperrimus*	22.4	measured image	23.7	measured image	18.4	measured image	21.1	measured image
Round Goby	*Neogobius melanostomus*	25.8	FishBase	26.6	FishBase	21.7	FishBase	24.7	FishBase
Ruffe	*Gymnocephalus cernua*	28.7	FishBase	26.8	FishBase	27.3	FishBase	30.5	FishBase
Sacramento Perch	*Archoplites interruptus*	27.8	FishBase	26.2	FishBase	29.8	FishBase	26.4	FishBase
Saugeye	*Sander vitreus X S. canadensis*	29.3	FishBase	24.6	FishBase	21.7	FishBase	24.3	FishBase
Sea Lamprey	*Petromyzon marinus*	-	-	-	-	7.2	FishBase	21.1	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	38.2	FishBase	20	FishBase	25.6	FishBase	20.7	FishBase
Smallmouth Bass	*Micropterus dolomieui*	27	FishBase	25.2	FishBase	26.7	FishBase	26.5	FishBase
Striped Bass	*Morone saxatilis*	25.7	FishBase	25.1	FishBase	25.1	FishBase	24.4	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	41.7	FishBase	32.3	FishBase	23.1	FishBase	25.4	FishBase

Walleye	*Sander vitreus*	26	FishBase	21.7	FishBase	15.5	FishBase	22.5	FishBase
Western Carp Gudgeon	*Hypseleotris klunzingeri*	26.9	measured image	26.1	measured image	19.4	measured image	26.1	measured image
White Crappie	*Pomoxis annularis*	27.6	FishBase	24.7	FishBase	36.4	FishBase	24.7	FishBase
White Sturgeon	*Acipenser transmontanus*	55.3	measured image	24	measured image	10.7	measured image	23.3	measured image
White Sucker	*Catostomus commersonii*	48.6	FishBase	20.1	FishBase	18	FishBase	19.9	FishBase
Yellow Bullhead	*Ameiurus natalis*	39.6	FishBase	21.1	FishBase	15.9	FishBase	22.3	FishBase
Yellow Perch	*Perca flavescens*	28.8	FishBase	22.4	FishBase	23.4	FishBase	22.7	FishBase
Zander	*Sander lucioperca*	25.6	FishBase	22.6	FishBase	18	FishBase	21.7	FishBase

A6. Continued.

Fish common name	Fish taxonomic name	ED (%)	ED source	PO (%)	PO source	CA	CA source
Alewife	*Alosa pseudoharengus*	30.3	FishBase	22.2	FishBase	2.0842	FishBase
American Eel	*Anguilla rostrata*	7.2	FishBase	21.7	FishBase	-	FishBase
Atlantic Herring	*Clupea harengus*	26.1	FishBase	23.5	FishBase	1.6200	FishBase
Atlantic Salmon	*Salmo salar*	16	FishBase	30.5	FishBase	2.0158	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	14.4	FishBase	22.4	FishBase	1.9754	FishBase
Bitterling	*Rhodeus sericeus*	33.3	FishBase	22.5	FishBase	1.3256	FishBase
Bloater	*Coregonus hoyi*	30.7	FishBase	22.8	FishBase	5.4162	FishBase
Bluegill	*Lepomis macrochirus*	22.8	FishBase	20.9	FishBase	1.6189	FishBase

Brook Trout	*Salvelinus fontinalis*	21.2	FishBase	26.3	FishBase	1.5382	FishBase
Brown Bullhead	*Ameiurus nebulosus*	12.2	FishBase	32.1	FishBase	1.1381	FishBase
Brown Trout	*Salmo trutta*	24.2	FishBase	24.2	FishBase	1.2533	FishBase
Bull Trout	*Salvelinus confluentus*	16.8	FishBase	39.6	FishBase	1.5174	FishBase
Burbot	*Lota lota*	12.4	FishBase	31	FishBase	0.7259	FishBase
Central Mudminnow	*Umbra limi*	21.9	FishBase	16.4	FishBase	1.1650	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	10.2	FishBase	29.9	FishBase	1.6366	FishBase
Common Carp	*Cyprinus carpio*	16.4	FishBase	28.1	FishBase	1.8462	FishBase
Crucian Carp	*Carassius carassius*	19.6	FishBase	23.2	FishBase	1.1844	FishBase
Eurasian Perch	*Perca fluviatilus*	22.4	FishBase	27.3	FishBase	1.5214	FishBase

European Brook Lamprey	*Lampetra planeri*	9.4	FishBase	33	FishBase	0.5551	FishBase
European Eel	*Anguilla anguilla*	12.5	FishBase	25	FishBase	-	FishBase
European Flounder	*Platichthys flesus*	17.7	FishBase	10.5	FishBase	0.6116	FishBase
Fathead Minnow	*Pimephales promelas*	29.2	FishBase	23	FishBase	1.5111	FishBase
Flathead Catfish	*Pylodictis olivaris*	10.4	FishBase	27.1	FishBase	1.1852	FishBase
Flathead Mullet	*Mugil cephalus*	20.9	FishBase	20	FishBase	2.5347	FishBase
Gizzard Shad	*Dorosoma cepedianum*	20	FishBase	21	FishBase	2.2204	FishBase
Goldfish	*Carrasius auratus*	25	FishBase	19.1	FishBase	1.9617	FishBase
Grass Carp	*Ctenopharyngodon idella*	20.8	FishBase	22.3	FishBase	1.5157	FishBase
Green Sunfish	*Lepomis cyanellus*	19.6	FishBase	25.2	FishBase	1.5881	FishBase

Humpback Chub	*Gila cypha*	11.9	FishBase	27.4	FishBase	2.0242	FishBase
Japanese Eel	*Anguilla japonica*	7.4	FishBase	13.9	FishBase	-	FishBase
Lake Trout	*Salvelinus namaycush*	11.8	FishBase	29.1	FishBase	2.1109	FishBase
Lake Whitefish	*Coregonus clupeaformis*	21.2	FishBase	23.5	FishBase	1.8018	FishBase
Largemouth Bass	*Micropterus salmoides*	15.3	FishBase	22.9	FishBase	1.2772	FishBase
Marbled Sculpin	*Cottus klamathensis*	24.4	measured image	22	measured image	0.8761	estimate (Prickly Sculpin)
Mississippi Paddlefish	*Polyodon spathula*	1.7	FishBase	47.7	FishBase	2.4140	FishBase
Northern Pike	*Esox lucius*	11.6	FishBase	39.5	FishBase	1.4425	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	9	FishBase	38.8	FishBase	1.4778	FishBase
Northern Redbelly Dace	*Chrosomus eos*	27.2	FishBase	22.3	FishBase	1.1485	FishBase

Northern Snakehead	*Channa argus*	12.4	FishBase	15.4	FishBase	1.0941	FishBase
Pallid Sturgeon	*Scaphirhynchus albus*	2.8	measured image	52.8	measured image	2.0593	estimate (Green Sturgeon (FishBase)
Pink Salmon	*Oncorhynchus gorbuscha*	12.3	FishBase	28.7	FishBase	2.4872	FishBase
Pit Sculpin	*Cottus pitensis*	25	measured image	17.5	measured image	0.8761	estimate (Prickly Sculpin)
Prickly Sculpin	*Cottus asper*	16.9	FishBase	21.6	FishBase	0.8761	FishBase
Pumpkinseed	*Lepomis gibbosus*	19.2	FishBase	28.2	FishBase	0.7211	FishBase
Rainbow Smelt	*Osmerus mordax*	24	FishBase	26	FishBase	2.3411	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	16	FishBase	35.1	FishBase	1.7317	FishBase
River Lamprey	*Lampetra fluviatilis*	8.6	measured image	34.3	measured image	0.8090	estimate (Sea Lamprey)
Rock Bass	*Ambloplites rupestris*	26.4	FishBase	27	FishBase	1.0471	FishBase

Rough Sculpin	*Cottus asperrimus*	25	measured image	18.8	measured image	0.8761	estimate (Prickly Sculpin)
Round Goby	*Neogobius melanostomus*	18.4	FishBase	26.5	FishBase	0.8926	FishBase
Ruffe	*Gymnocephalus cernua*	17.6	FishBase	30.2	FishBase	1.4543	FishBase
Sacramento Perch	*Archoplites interruptus*	30.9	FishBase	18	FishBase	0.9994	FishBase
Saugeye	*Sander vitreus X S. canadensis*	14.8	FishBase	26.8	FishBase	1.2630	FishBase
Sea Lamprey	*Petromyzon marinus*	4.5	FishBase	36.4	FishBase	0.8090	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	15.8	FishBase	18.3	FishBase	2.4412	FishBase
Smallmouth Bass	*Micropterus dolomieui*	15.1	FishBase	27	FishBase	1.4301	FishBase
Striped Bass	*Morone saxatilis*	16.3	FishBase	29.6	FishBase	2.0669	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	24	FishBase	32.9	FishBase	2.0399	FishBase

Walleye	*Sander vitreus*	19.7	FishBase	23.4	FishBase	1.2939	FishBase
Western Carp Gudgeon	*Hypseleotris klunzingeri*	22.9	measured image	31.4	measured image	1.3081	estimate (Plains Killifish (FishBase))
White Crappie	*Pomoxis annularis*	19	FishBase	24.8	FishBase	1.6196	FishBase
White Sturgeon	*Acipenser transmontanus*	5.7	measured image	37.1	measured image	2.0593	estimate (Green Sturgeon (FishBase))
White Sucker	*Catostomus commersonii*	21.4	FishBase	42	FishBase	1.5910	FishBase
Yellow Bullhead	*Ameiurus natalis*	8	FishBase	23.2	FishBase	0.8676	FishBase
Yellow Perch	*Perca flavescens*	19.5	FishBase	24.1	FishBase	1.2341	FishBase
Zander	*Sander lucioperca*	14.5	FishBase	19.8	FishBase	1.4491	FishBase

A6. Continued.

Fish common name	Fish taxonomic name	BS	BS source	MP	MP source	HP	HP source
Alewife	*Alosa pseudoharengus*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
American Eel	*Anguilla rostrata*	eel-like	FishBase	terminal/superior	FishBase	demersal	FishBase
Atlantic Herring	*Clupea harengus*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Atlantic Salmon	*Salmo salar*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	fusiform/normal	FishBase	terminal/superior	observation	benthopelagic/pelagic	FishBase
Bitterling	*Rhodeus sericeus*	fusiform/normal	FishBase	inferrior	FishBase	benthopelagic/pelagic	FishBase
Bloater	*Coregonus hoyi*	fusiform/normal	estimate (Salmon)	terminal/superior	observation	demersal	FishBase
Bluegill	*Lepomis macrochirus*	short/deep	FishBase	terminal/superior	estimate (Largemouth Bass)	benthopelagic/pelagic	FishBase

Brook Trout	*Salvelinus fontinalis*	fusiform/normal	FishBase	terminal/superior	observation	demersal	FishBase
Brown Bullhead	*Ameiurus nebulosus*	fusiform/normal	FishBase	terminal/superior	Scott and Crossman 1973	demersal	FishBase
Brown Trout	*Salmo trutta*	fusiform/normal	estimate (Salmon)	terminal/superior	Scott and Crossman 1973	benthopelagic/pelagic	FishBase
Bull Trout	*Salvelinus confluentus*	fusiform/normal	estimate (Dolly Varden (FishBase))	terminal/superior	estimate (Dolly Varden)	benthopelagic/pelagic	FishBase
Burbot	*Lota lota*	elongate	FishBase	terminal/superior	FishBase	demersal	FishBase
Central Mudminnow	*Umbra limi*	elongate	observation	terminal/superior	observation	demersal	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Common Carp	*Cyprinus carpio*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Crucian Carp	*Carassius carassius*	fusiform/normal	FishBase	terminal/superior	observation	demersal	FishBase
Eurasian Perch	*Perca fluviatilus*	fusiform/normal	FishBase	terminal/superior	FishBase	demersal	FishBase

European Brook Lamprey	*Lampetra planeri*	eel-like	FishBase	inferrior	FishBase	demersal	FishBase
European Eel	*Anguilla anguilla*	eel-like	FishBase	terminal/superior	FishBase	demersal	FishBase
European Flounder	*Platichthys flesus*	short/deep	FishBase	terminal/superior	FishBase	demersal	FishBase
Fathead Minnow	*Pimephales promelas*	fusiform/normal	FishBase	terminal/superior	FishBase	demersal	FishBase
Flathead Catfish	*Pylodictis olivaris*	fusiform/normal	estimate (Channel Catfish (FishBase))	terminal/superior	observation	demersal	FishBase
Flathead Mullet	*Mugil cephalus*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Gizzard Shad	*Dorosoma cepedianum*	fusiform/normal	FishBase	inferrior	FishBase	benthopelagic/pelagic	FishBase
Goldfish	*Carrasius auratus*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Grass Carp	*Ctenopharyngodon idella*	fusiform/normal	FishBase	inferrior	FishBase	demersal	FishBase
Green Sunfish	*Lepomis cyanellus*	short/deep	FishBase	terminal/superior	Scott and Crossman 1973	benthopelagic/pelagic	FishBase

Humpback Chub	*Gila cypha*	elongate	observation	terminal/superior	observation	benthopelagic/pelagic	FishBase
Japanese Eel	*Anguilla japonica*	eel-like	FishBase	terminal/superior	observation	demersal	FishBase
Lake Trout	*Salvelinus namaycush*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Lake Whitefish	*Coregonus clupeaformis*	fusiform/normal	FishBase	inferrior	FishBase	demersal	FishBase
Largemouth Bass	*Micropterus salmoides*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Marbled Sculpin	*Cottus klamathensis*	elongate	estimate (Slimy Sculpin (FishBase))	terminal/superior	observation	demersal	FishBase
Mississippi Paddlefish	*Polyodon spathula*	elongate	FishBase	inferrior	observation	demersal	FishBase
Northern Pike	*Esox lucius*	elongate	FishBase	terminal/superior	observation	demersal	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Northern Redbelly Dace	*Chrosomus eos*	fusiform/normal	observation	terminal/superior	observation	demersal	FishBase

Northern Snakehead	*Channa argus*	fusiform/normal	FishBase	terminal/superior	observation	benthopelagic/pelagic	FishBase
Pallid Sturgeon	*Scaphirhynchus albus*	elongate	FishBase	inferrior	observation	demersal	FishBase
Pink Salmon	*Oncorhynchus gorbuscha*	fusiform/normal	FishBase	terminal/superior	FishBase	demersal	FishBase
Pit Sculpin	*Cottus pitensis*	elongate	estimate (Slimy Sculpin (FishBase))	terminal/superior	observation	demersal	FishBase
Prickly Sculpin	*Cottus asper*	elongate	FishBase	terminal/superior	observation	demersal	FishBase
Pumpkinseed	*Lepomis gibbosus*	short/deep	FishBase	terminal/superior	Scott and Crossman 1973	benthopelagic/pelagic	FishBase
Rainbow Smelt	*Osmerus mordax*	elongate	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase
River Lamprey	*Lampetra fluviatilis*	eel-like	FishBase	inferrior	FishBase	demersal	FishBase
Rock Bass	*Ambloplites rupestris*	short/deep	FishBase	terminal/superior	observation	demersal	FishBase

Rough Sculpin	*Cottus asperrimus*	elongate	estimate (Slimy Sculpin (FishBase))	terminal/superior	observation	demersal	FishBase
Round Goby	*Neogobius melanostomus*	fusiform/normal	FishBase	terminal/superior	observation	demersal	FishBase
Ruffe	*Gymnocephalus cernua*	fusiform/normal	FishBase	inferior	observation	demersal	FishBase
Sacramento Perch	*Archoplites interruptus*	short/deep	estimate (Bluegill)	terminal/superior	California Fish Website 2015	benthopelagic/pelagic	FishBase
Saugeye	*Sander vitreus X S. canadensis*	elongate	estimate (Walleye)	terminal/superior	estimate (Walleye)	demersal	FishBase
Sea Lamprey	*Petromyzon marinus*	eel-like	FishBase	inferior	FishBase	demersal	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	fusiform/normal	FishBase	terminal/superior	observation	benthopelagic/pelagic	FishBase
Smallmouth Bass	*Micropterus dolomieui*	fusiform/normal	FishBase	terminal/superior	Scott and Crossman 1973	benthopelagic/pelagic	FishBase
Striped Bass	*Morone saxatilis*	fusiform/normal	FishBase	terminal/superior	observation	demersal	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	fusiform/normal	FishBase	terminal/superior	FishBase	benthopelagic/pelagic	FishBase

Walleye	*Sander vitreus*	elongate	FishBase	terminal/superior	FishBase	demersal	FishBase
Western Carp Gudgeon	*Hypseleotris klunzingeri*	elongate	observation	terminal/superior	observation	demersal	FishBase
White Crappie	*Pomoxis annularis*	short/deep	Scott and Crossman 1973	terminal/superior	Scott and Crossman 1973	demersal	FishBase
White Sturgeon	*Acipenser transmontanus*	elongate	FishBase	inferrior	observation	demersal	FishBase
White Sucker	*Catostomus commersonii*	fusiform/normal	observation	inferior	observation	demersal	FishBase
Yellow Bullhead	*Ameiurus natalis*	fusiform/normal	estimate (Brown Bullhead)	terminal/superior	Scott and Crossman 1973	demersal	FishBase
Yellow Perch	*Perca flavescens*	fusiform/normal	observation	terminal/superior	Scott and Crossman 1973	benthopelagic/pelagic	FishBase
Zander	*Sander lucioperca*	fusiform/normal	FishBase	terminal/superior	observation	benthopelagic/pelagic	FishBase

A6. Continued.

Fish common name	Fish taxonomic name	ML (years)	ML source	MF (eggs)	MF source
Alewife	*Alosa pseudoharengus*	9	FishBase	660000	FishBase
American Eel	*Anguilla rostrata*	43	FishBase	19920000	FishBase
Atlantic Herring	*Clupea harengus*	25	FishBase	301000	FishBase
Atlantic Salmon	*Salmo salar*	13	FishBase	26000	FishBase
Bighead Carp	*Hypophthalmichthys nobilis*	20	FishBase	1100000	FishBase
Bitterling	*Rhodeus sericeus*	5	FishBase	500	FishBase
Bloater	*Coregonus hoyi*	10	FishBase	18768	FishBase
Bluegill	*Lepomis macrochirus*	10	FishBase	38184	Scott and Crossman 1973

Brook Trout	*Salvelinus fontinalis*	24	FishBase	5000	FishBase
Brown Bullhead	*Ameiurus nebulosus*	9	FishBase	13000	Scott and Crossman 1973
Brown Trout	*Salmo trutta*	38	FishBase	10000	FishBase
Bull Trout	*Salvelinus confluentus*	24	DFO 2014	5000	Hammond 2004
Burbot	*Lota lota*	20	FishBase	5000000	FishBase
Central Mudminnow	*Umbra limi*	4	FishBase	1500	FishBase
Chinook Salmon	*Oncorhynchus tshawytscha*	9	FishBase	13619	FishBase
Common Carp	*Cyprinus carpio*	38	FishBase	2208000	FishBase
Crucian Carp	*Carassius carassius*	10	FishBase	300000	FishBase
Eurasian Perch	*Perca fluviatilus*	22	FishBase	300000	FishBase

European Brook Lamprey	*Lampetra planeri*	7	FishBase	10000	FishBase
European Eel	*Anguilla anguilla*	88	FishBase	3000000	FishBase
European Flounder	*Platichthys flesus*	15	FishBase	2920230	FishBase
Fathead Minnow	*Pimephales promelas*	5	FishBase	10164	FishBase
Flathead Catfish	*Pylodictis olivaris*	20	FishBase	100000	FishBase
Flathead Mullet	*Mugil cephalus*	16	FishBase	7000000	FishBase
Gizzard Shad	*Dorosoma cepedianum*	10	FishBase	543912	FishBase
Goldfish	*Carrasius auratus*	41	FishBase	400000	FishBase
Grass Carp	*Ctenopharyngodon idella*	21	FishBase	1500000	FishBase
Green Sunfish	*Lepomis cyanellus*	9	FishBase	50000	University of Michigan Critter Catalogue 2015

Humpback Chub	*Gila cypha*	30	National Park Service 2015	2523	Hamman 1982 (mean value)
Japanese Eel	*Anguilla japonica*	20	USGS 2015	5700000	USGS 2015
Lake Trout	*Salvelinus namaycush*	50	FishBase	17000	FishBase
Lake Whitefish	*Coregonus clupeaformis*	50	FishBase	150000	Eakins 2015
Largemouth Bass	*Micropterus salmoides*	23	FishBase	25000	FishBase
Marbled Sculpin	*Cottus klamathensis*	5	FishBase	650	California Fish Website 2015
Mississippi Paddlefish	*Polyodon spathula*	55	FishBase	608650	FishBase
Northern Pike	*Esox lucius*	30	FishBase	600000	FishBase
Northern Pikeminnow	*Ptychocheilus oregonensis*	11	FishBase	36359	Knutsen and Ward 1998
Northern Redbelly Dace	*Chrosomus eos*	8	Scott and Crossman 1973	6450	FishBase

Northern Snakehead	*Channa argus*	17	estimate based on correlations	15000	USGS 2012
Pallid Sturgeon	*Scaphirhynchus albus*	41	FishBase	170000	FishBase
Pink Salmon	*Oncorhynchus gorbuscha*	3	FishBase	2000	FishBase
Pit Sculpin	*Cottus pitensis*	5	FishBase	320	Daniels 1987
Prickly Sculpin	*Cottus asper*	7	FishBase	10980	FishBase
Pumpkinseed	*Lepomis gibbosus*	12	FishBase	5000	Scott and Crossman 1973
Rainbow Smelt	*Osmerus mordax*	7	FishBase	69600	FishBase
Rainbow Trout	*Oncorhynchus mykiss*	11	FishBase	12749	FishBase
River Lamprey	*Lampetra fluviatilis*	10	FishBase	42000	FishBase
Rock Bass	*Ambloplites rupestris*	18	FishBase	11000	FishBase

Rough Sculpin	*Cottus asperrimus*	5	FishBase	580	California Fish Website 2015
Round Goby	*Neogobius melanostomus*	4	FishBase	5000	FishBase
Ruffe	*Gymnocephalus cernua*	10	FishBase	200000	FishBase
Sacramento Perch	*Archoplites interruptus*	9	FishBase	125000	California Fish Website 2015
Saugeye	*Sander vitreus X S. canadensis*	18	FishBase	210000	FishBase
Sea Lamprey	*Petromyzon marinus*	11	FishBase	304000	FishBase
Silver Carp	*Hypophthalmichthys molitrix*	10	Indiana Government 2005	500000	FishBase
Smallmouth Bass	*Micropterus dolomieui*	26	FishBase	14000	FishBase
Striped Bass	*Morone saxatilis*	30	FishBase	4500000	FishBase
Threespine Stickleback	*Gasterosteus aculeatus*	8	FishBase	1300	FishBase

Walleye	*Sander vitreus*	29	FishBase	612000	FishBase
Western Carp Gudgeon	*Hypseleotris klunzingeri*	2	FishBase (estimate by life history tool)	2000	Murray-Darling Basin Authority 2007 (value for genus)
White Crappie	*Pomoxis annularis*	10	FishBase	147800	FishBase
White Sturgeon	*Acipenser transmontanus*	104	FishBase	4000000	FishBase
White Sucker	*Catostomus commersonii*	12	FishBase	50000	FishBase
Yellow Bullhead	*Ameiurus natalis*	4	FishBase	4270	Scott and Crossman 1973
Yellow Perch	*Perca flavescens*	11	FishBase	109000	FishBase
Zander	*Sander lucioperca*	17	FishBase	2957400	FishBase

A6. sources of data:

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A7. Variable importance scores determined by classification random forests in Chapter 3. Underlined values were considered important. K = von Bertalanffy growth coefficient, TRL = trophic level, TG = trophic guild, AM = age at maturity, ST = swim type, MW = maximum weight, MTL = maximum total length, SL = standard length to total length ratio, FL = fork length to total length ratio, PA = pre-anal length to total length ratio, PD = pre-dorsal length to total length ratio, PPEL = pre-pelvic length to total length ratio, BD = body depth to total length ratio, HL = head length to total length ratio, ED = eye diameter to head length ratio, PO = pre-orbital length to head length ratio, CA = caudal fin aspect ratio, BS = body shape, MP = mouth position, HP = habitat preference, ML = maximum lifespan, MF = maximum fecundity.

Variable	mt		mt, iteration 2		s		s, iteration 2		r1, seed1	r2, seed1	r3, seed1	r4, seed1	r5, seed1	r6, seed1	r7, seed1	r8, seed1	r9, seed1	r10, seed1
	seed1	seed2	seed1	seed2	seed1	seed2	seed1	seed2										
K	-	-	-	-	<u>0.0072</u>	<u>0.0074</u>	<u>0.0208</u>	<u>0.0213</u>	-	-	-	-	-	-	-	-	-	-
TRL	-0.0007	-0.0007	-	-	-0.0012	-0.0011	-	-	-0.0015	0.0001	0.0004	-0.0006	0.001	-0.0004	0.0007	-0.002	-0.0023	-0.0004
TG	<u>0.0039</u>	<u>0.0037</u>	<u>0.0066</u>	<u>0.0062</u>	-0.001	-0.0013	-	-	0.0012	0.0001	0.0012	<u>0.0085</u>	-0.0003	0.0007	-0.0003	<u>0.0074</u>	<u>0.0073</u>	0.0016
AM	<u>0.0154</u>	<u>0.0151</u>	<u>0.0218</u>	<u>0.0216</u>	<u>0.0096</u>	<u>0.0091</u>	<u>0.0254</u>	<u>0.0248</u>	<u>0.0083</u>	<u>0.0073</u>	<u>0.0059</u>	<u>0.0245</u>	<u>0.0134</u>	<u>0.0201</u>	<u>0.0049</u>	<u>0.0118</u>	<u>0.0118</u>	<u>0.0102</u>
ST	0.0003	-0.0003			-0.0006	-0.0005	-	-	-0.0008	0.0015	0.0003	0.0002	0.0002	-0.0003	0.0011	-0.0004	0.0001	-0.0005
MW	<u>0.0037</u>	<u>0.0041</u>	<u>0.0057</u>	<u>0.0054</u>	0.0016	0.0017	-	-	0.0017	<u>0.0081</u>	0.0005	<u>0.0031</u>	<u>0.0032</u>	<u>0.007</u>	<u>0.0084</u>	0.0009	0.0014	<u>0.0022</u>
MTL	<u>0.0092</u>	<u>0.0097</u>	<u>0.012</u>	<u>0.0118</u>	<u>0.0022</u>	0.0021	-	-	<u>0.0053</u>	<u>0.0122</u>	<u>0.0027</u>	<u>0.0092</u>	<u>0.0125</u>	<u>0.0166</u>	<u>0.0099</u>	<u>0.0041</u>	<u>0.0046</u>	<u>0.0116</u>
SL	-0.0003	-0.0002	-	-	-0.001	-0.0011	-	-	-0.0008	0.0004	-0.0006	<u>0.0029</u>	0.0007	0.0003	-0.0004	-0.0003	-0.0001	0.0001
FL	0.002	0.0021	-	-	-0.0008	-0.0003	-	-	<u>0.0039</u>	-0.0007	<u>0.0048</u>	<u>0.0021</u>	-0.0006	0.0014	<u>0.0029</u>	<u>0.0039</u>	-0.0015	-0.0005
PA	-	-	-	-	-0.0014	-0.0015	-	-	-	-	-	-	-	-	-	-	-	-
PD	0.0017	<u>0.0023</u>	-	-	0.0013	0.0011	-	-	-0.002	0.0003	<u>0.0067</u>	<u>0.006</u>	0.0007	<u>0.0067</u>	<u>0.0029</u>	0.0001	-0.0004	0.0002

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
PPEL	-	-	-	-	-0.0005	-0.0006	-	-	-	-	-	-	-	-	-	-	-	-
PPEC	-	-	-	-	-0.0015	-0.0012	-	-	-	-	-	-	-	-	-	-	-	-
BD	-0.0021	-0.0021	-	-	-0.0017	-0.0016	-	-	-0.0014	-0.0011	-0.0018	-0.001	-0.0023	-0.0016	-0.0006	-0.0024	-0.0017	-0.0019
HL	-0.0002	-0.0003	-	-	-0.0013	-0.0012	-	-	-0.001	-0.0014	0.001	0.0004	-0.0006	-0.0007	-0.0007	0.0003	-0.0017	-0.0004
ED	<u>0.0033</u>	<u>0.0033</u>	<u>0.0027</u>	<u>0.0031</u>	<u>0.0038</u>	<u>0.0031</u>	<u>0.0097</u>	<u>0.0082</u>	-0.0005	<u>0.0047</u>	<u>0.0064</u>	<u>0.0022</u>	<u>0.0069</u>	0.0002	<u>0.0054</u>	<u>0.0058</u>	0.0014	<u>0.0102</u>
PO	-0.0003	-0.0002	-	-	0.0003	0.0002	-	-	0.0014	0.0002	0	-0.0006	-0.0002	-0.0009	0.0002	-0.0001	0.0001	0.0006
CA	-	-	-	-	0.001	0.001	-	-	-	-	-	-	-	-	-	-	-	-
BS	0.0018	<u>0.0025</u>	-	-	-0.001	-0.001	-	-	0.0001	<u>0.0024</u>	<u>0.0025</u>	0.0001	<u>0.005</u>	<u>0.002</u>	<u>0.0075</u>	0.0008	-0.0012	<u>0.0028</u>
MP	-0.0002	-0.0002	-	-	0	0	-	-	-0.0003	-0.0001	0	0	-0.0002	-0.0001	0	0	-0.0002	-0.0002
HP	-0.0021	-0.0021	-	-	0.0018	0.0023	-	-	-0.0015	-0.0019	-0.0017	-0.0013	-0.0019	-0.0019	-0.0013	-0.002	-0.002	-0.0017
ML	<u>0.008</u>	<u>0.0085</u>	<u>0.0123</u>	<u>0.0135</u>	<u>0.0057</u>	<u>0.0052</u>	<u>0.0153</u>	<u>0.0158</u>	<u>0.0025</u>	<u>0.0123</u>	<u>0.0021</u>	<u>0.0059</u>	<u>0.0148</u>	<u>0.0074</u>	<u>0.0089</u>	<u>0.0035</u>	<u>0.005</u>	<u>0.0139</u>
MF	-0.0012	-0.0013	-	-	-0.0012	-0.0011	-	-	-0.0016	-0.0008	-0.001	-0.001	-0.0012	-0.0002	-0.0007	-0.0009	-0.0012	-0.0003

A8. Variable importance scores determined by regression random forests in Chapter 3. Underlined values were considered important. K = von Bertalanffy growth coefficient, TRL = trophic level, TG = trophic guild, AM = age at maturity, ST = swim type, MW = maximum weight, MTL = maximum total length, SL = standard length to total length ratio, FL = fork length to total length ratio, PA = pre-anal length to total length ratio, PD = pre-dorsal length to total length ratio, PPEL = pre-pelvic length to total length ratio, BD = body depth to total length ratio, HL = head length to total length ratio, ED = eye diameter to head length ratio, PO = pre-orbital length to head length ratio, CA = caudal fin aspect ratio, BS = body shape, MP = mouth position, HP = habitat preference, ML = maximum lifespan, MF = maximum fecundity.

Variable	mt seed1	mt seed2	mt, iteration 2 seed1	mt, iteration 2 seed2	s seed1	s seed2	s, iteration 2 seed1	s, iteration 2 seed2	r1, seed1	r2, seed1	r3, seed1	r4, seed1	r5, seed1	r6, seed1	r7, seed1	r8, seed1	r9, seed1	r10, seed1
K	-	-	-	-	3.75E-07	3.72E-07	3.42E-07	3.39E-07	-	-	-	-	-	-	-	-	-	-
TRL	-1.38E-08	-1.13E-08	-	-	-2.40E-08	-2.77E-08	-	-	-1.52E-08	-3.09E-08	3.27E-08	-2.43E-08	-3.20E-08	-3.08E-08	-8.68E-09	-8.16E-09	-2.22E-08	-2.86E-08
TG	2.02E-07	1.99E-07	2.57E-07	2.51E-07	-1.85E-08	-1.80E-08	-	-	1.06E-07	1.40E-07	4.03E-08	3.96E-07	-1.59E-08	2.01E-08	-4.02E-09	3.63E-07	4.60E-07	7.39E-08
AM	1.53E-07	1.52E-07	2.82E-07	2.85E-07	5.62E-08	5.52E-08	2.23E-07	2.08E-07	3.22E-07	2.50E-07	4.65E-08	7.74E-08	1.18E-07	4.58E-08	1.48E-07	2.25E-07	1.25E-07	1.80E-07
ST	1.08E-08	1.01E-08	-	-	-4.35E-09	-4.40E-09	-	-	2.84E-09	1.45E-08	2.97E-10	-5.42E-12	-2.17E-09	-5.36E-09	8.98E-09	-7.25E-10	2.50E-08	5.58E-10
MW	6.25E-09	7.83E-09	-	-	2.17E-08	2.10E-08	-	-	8.08E-09	2.39E-08	4.74E-08	8.47E-09	-7.76E-09	9.12E-09	4.59E-08	1.51E-08	-1.12E-08	-5.69E-09
MTL	8.81E-08	8.52E-08	1.14E-07	1.16E-07	6.95E-08	7.78E-08	9.27E-08	1.00E-07	8.52E-08	1.71E-07	1.16E-07	1.52E-07	3.98E-08	1.44E-07	2.93E-07	1.10E-07	2.77E-08	4.44E-08
SL	-4.08E-09	-6.30E-09	-	-	-2.61E-08	-2.55E-08	-	-	1.29E-08	-2.57E-08	-1.01E-08	5.11E-09	-6.96E-09	-1.78E-08	-2.39E-08	1.26E-08	-7.80E-09	-1.48E-08
FL	-9.53E-09	-8.55E-09	-	-	-1.96E-08	-1.68E-08	-	-	-7.32E-09	-4.00E-09	6.56E-09	-1.97E-08	-3.11E-08	-2.59E-08	-1.40E-08	1.26E-09	5.86E-09	-2.17E-08
PA	-	-	-	-	-1.52E-08	-1.32E-08	-	-	-	-	-	-	-	-	-	-	-	-
PD	-3.33E-08	-2.94E-08	-	-	-2.21E-08	-2.86E-08	-	-	-6.29E-08	-3.40E-08	4.54E-08	-3.43E-08	-4.12E-08	-4.49E-08	-4.15E-09	-2.90E-08	-2.55E-08	-5.64E-08

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
PPEL	-	-	-	-	-1.09E-08	-1.31E-08	-	-	-	-	-	-	-	-	-	-	-	-
PPEC	-	-	-	-	-3.65E-08	-2.79E-08	-	-	-	-	-	-	-	-	-	-	-	-
BD	-2.16E-08	-1.98E-08	-	-	-1.79E-08	-1.94E-08	-	-	-2.05E-08	-1.75E-08	-1.63E-08	-3.54E-08	-2.94E-08	-2.49E-08	-3.82E-09	-2.13E-08	-2.01E-08	-4.99E-08
HL	-2.22E-08	-2.35E-08	-	-	-2.31E-08	-2.12E-08	-	-	-3.04E-08	-3.57E-08	-1.02E-08	-2.15E-08	-3.23E-08	-3.32E-08	-8.25E-09	-1.63E-08	-2.86E-08	-3.30E-08
ED	3.98E-07	4.04E-07	3.31E-07	3.20E-07	4.58E-07	4.75E-07	4.97E-07	5.06E-07	3.89E-07	6.65E-07	4.91E-07	2.35E-07	3.17E-07	5.62E-08	5.36E-07	6.17E-07	3.84E-07	4.55E-07
PO	-1.06E-08	-6.59E-09	-	-	-5.03E-09	-4.72E-09	-	-	3.12E-09	-1.58E-08	8.53E-09	-1.67E-08	-3.40E-08	-3.24E-08	9.93E-09	-4.00E-09	-1.39E-08	-6.40E-09
CA	-	-	-	-	-5.68E-09	-7.60E-09	-	-	-	-	-	-	-	-	-	-	-	-
BS	6.46E-10	1.68E-09	-	-	-3.62E-09	-3.91E-09	-	-	1.60E-08	-8.43E-10	-3.17E-09	3.73E-09	-4.93E-09	6.68E-09	-1.74E-09	3.19E-09	-3.07E-09	-3.09E-09
MP	-2.04E-09	-2.79E-09	-	-	-8.98E-10	-5.72E-10	-	-	1.67E-09	-3.23E-09	0	-9.30E-10	-4.57E-09	-1.68E-09	-1.60E-10	0	-3.36E-09	-3.27E-09
HP	-3.14E-08	-3.12E-08	-	-	-2.70E-08	-3.18E-08	-	-	-3.05E-08	-3.46E-08	-1.74E-08	-2.73E-08	-2.38E-08	-2.89E-08	-2.15E-08	-2.35E-08	-3.65E-08	-2.79E-08
ML	3.65E-08	3.45E-08	3.33E-08	3.76E-08	7.81E-08	7.23E-08	9.87E-08	1.01E-07	1.17E-07	-1.04E-08	6.63E-08	3.45E-08	-2.38E-08	-3.04E-08	1.20E-07	7.39E-08	-1.79E-08	2.44E-08
MF	-1.04E-08	-8.47E-09	-	-	1.48E-09	3.62E-10	-	-	-4.73E-09	2.97E-08	-1.32E-09	-4.27E-09	-1.87E-08	-1.13E-08	-9.72E-10	-3.90E-09	-6.46E-09	-1.52E-08

A9. R scripts used in this research.
##

*Scripts refer to csv files saved in Microsoft Excel
*Highlighted content can be changed to your specifications

##

FITTING THE ALLOMETRIC PART OF THE METABOLIC EQUATION

#this procedure uses a Microsoft Excel file containing two columns of data: metabolic_data is the y-variable, and fish_weight_data is the x-variable

#import and look at the data

data_name=read.csv("file location")

#look at the plot

plot(metabolic_data~fish_weight_data,data_name)

#choose some starting values based on similar species (these are the values R will calculate for you by doing the fit)

RA=0.0053
RB=-0.299

#There should be no activity component yet, as data should be at standard rates. If this is not the case, divide data by the activity multiplier of your choice to reduce from routine to standard.

#do the fit

fit_name=nls(metabolic_data~RA*fish_weight_data^(RB),data_name,start=list(RA=RA,RB=RB))

#summarise the fit

summary(fit_name)

##

FITTING METABOLIC f(T) FORM 1, (temperature > RTL)
#this procedure uses a Microsoft Excel file containing two columns of data: metabolic_data is the y-variable, and water_temperature_data is the x-variable

#import the data

data_name=read.csv("file_location")

#look at the plot

plot(metabolic_data~water_temperature_data,data_name)

#choose a starting value based on a similar species (this is the value R will calculate for you by doing the fit)

RQ=0.06

#do the fit (RA and RB are calculated using the allometric fit (or can be set to whatever you choose (i.e. based on similar species) if there wasn't enough data to do an allometric fit), fish_weight is whatever weight you are using; RTO, RK1, and RK4 are set to whatever you choose (i.e. based on similar species or literature))

fit_name=nls(metabolic_data~RA*fish_weight^(RB)*(exp(RQ*water_temperature_data))*(exp(RTO*(RK1*fish_weight^RK4))),data_name,start=list(RQ=RQ))

#summarise the fit

summary(fit_name)

##

FITTING METABOLIC f(T) FORM 1 (temperature ≤ RTL)

#this procedure uses a Microsoft Excel file containing two columns of data: metabolic_data is the y-variable, and water_temperature_data is the x-variable

#import the data

data_name=read.csv("file_location")

#look at the plot

plot(metabolic_data~water_temperature_data,data_name)

#choose a starting value based on a similar species (this is the value R will calculate for you by doing the fit)

RQ=0.06

#do the fit (RA and RB are calculated using the allometric fit (or can be set to whatever you choose (i.e. based on similar species) if there wasn't enough data to do an allometric fit), fish_weight is whatever weight you are using; RTO, RK1, RK4 , ACT, and BACT are set to whatever you choose (i.e. based on similar species or literature))

fit_name=nls(metabolic_data~RA*fish_weight^(RB)*(exp(RQ*water_temperature_data))*(exp(RTO*(ACT*fish_weight^RK4*exp(BACT*water_temperature_data)))),data_name,start=list(RQ=RQ))

#summarise the fit

summary(fit_name)

###

FITTING METABOLIC f(T) FORM 2

#this procedure uses a Microsoft Excel file containing two columns of data: metabolic_data is the y-variable, and water_temperature_data is the x-variable

#import the data

data_name=read.csv("file_location")

#look at the plot

plot(metabolic_data~water_temperature_data,data_name)

#choose a starting value based on a similar species (this is the value R will calculate for you by doing the fit)

RQ=0.06

#do the fit (RA and RB are calculated using the allometric fit (or can be set to whatever you choose (i.e. based on similar species) if there wasn't enough data to do an allometric fit), fish_weight is whatever weight you are using; RTM, RTO, and ACT are set to whatever you choose (i.e. based on similar species or literature))
#do the fit
fit=nls(metabolic_data~RA*fish_weight^(RB)*((RTM-water_temperature_data)/(RTM-RTO))^(((log(RQ)*(RTM-RTO))^2*(1+(1+40/(log(RQ)*(RTM-RTO+2)))^0.5)^2)/400)*exp((((log(RQ)*(RTM-RTO))^2*(1+(1+40/(log(RQ)*(RTM-RTO+2)))^0.5)^2)/400)*(1-((RTM-water_temperature_data)/(RTM-RTO))))*ACT,data_name,start=list(RQ=RQ))

#summarise the fit

summary(fit)

##

RANDOM FOREST

#this procedure uses a Microsoft Excel file containing multiple columns of data: metabolic_data is the y-variable, and a period (.) refers to all the x-variables (fish traits) collectively, so no need to type all the headings in

#load the party package

library(party)

#choose your seed number (the variable importance procedure must be run at two different seeds to check for consistency of importance results. If results are not consistent, you should increase the number of trees in the forest (i.e. ntree))

set.seed(1)

#import the data

data_name=read.csv("file_location")

#make the forest. The "control=cforest_unbiased" option makes the random forest unbiased to continuous vs. categorical data as well as categorical data with differing numbers of levels. Set mtry and ntree to whatever you choose. Default mtry using cforest is 5 for technical reasons

random_forest_name=cforest(metabolic_data~.,data=data_name,control=cforest _unbiased(mtry=3,ntree=20000))

#run a variable importance procedure. The "conditional=TRUE" option is used when you think you may have correlated x-variables. This may take around 30-40 minutes depending on your computer, how large your data set is, and the number of trees (i.e. ntree) you specified. "conditional=FALSE" is quicker, but does not account for correlations between x-variables

importance=varimp(random_forest_name,conditional=TRUE)

#view the importance output as a dotchart

importance
dotchart(sort(importance),col="darkblue", pch=16, cex=1.1)

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#add a red, dashed, vertical line to the threshold area (absolute value of minimum importance score).

abline(v=abs(min(importance)),col="red",lty="longdash",lwd=2)

#create a csv table of variable importance scores (this will save somewhere on your computer… "documents" I think.

write.csv(importance,"title_of_the_csv_file")

##

MAKING PREDICTIONS FOR OUT-OF-BAG (OOB) SAMPLES USING RANDOM FOREST

#after you build a random forest, this procedure is used to test it using OOB samples

#predict metabolic rates of out-of-bag (OOB) samples

predicted=predict(random_forest_name,OOB=TRUE)
predicted

##

MAKING PREDICTIONS FOR AN INDEPENDENT VALIDATION DATA SET USING RANDOM FOREST

#after you build a random forest, this procedure is used to test it using an independent validation data set. Once your random forest is built, this procedure uses a Microsoft Excel file containing multiple columns of data: metabolic_data is now the y-variable in the validation data set.

#load the testing data
test_data_name=read.csv("file_location")

#predict metabolic rates of test_data_name (for some reason I still needed the "OOB=TRUE" option even though I wasn't using OOB samples)

predicted=predict(random_forest_name,testing_data_name,OOB=TRUE)
predicted

#if your metabolic data is categorical, you can make a confusion matrix (metabolic_data refers to the actual metabolic rates in test_data_name)

table(testing_data_name$metabolic_data,predicted)

##

CALCULATING RMSE OF RANDOM FOREST AS A MEANS TO TEST DIFFERENT MTRY AND NTREE VALUES

#load caret package

library(caret)

#import the data

data_name=read.csv("file_location")

#set the seed

set.seed(1)

#train the model. Here I use 200 trees and try mtry values of 1 through 5. I haven't found a way to tune ntree… from the sounds of it, it is untuneable using the caret package, so you have to repeat this procedure for any other values of ntree you want to test

model=train(metabolic_data~.,data=data_name,method="cforest",controls=cforest_unbiased(ntree=200),tuneGrid=data.frame(mtry=(1:5)),trControl=trainControl(method="oob"))

#view the results. The smaller mse, the better.

model

##

CLASSIFICATION TREE

#this procedure uses two Microsoft Excel files, one containing the training data (training_data), and the other containing the testing data (testing_data). Both files contain multiple columns of data: metabolic_data is the y-variable, and a period (.) refers to all the x-variables (fish traits) collectively, so no need to type all the headings in

#load rpart (used to make the tree)

library(rpart)

```r
#load partykit (used to graph the tree)

library(partykit)

#import the data

training_data=read.csv("file_location")

testing_data=read.csv("file_location")

#create a new data set containing only the y-variables (metabolic_data) from the
testing set (testing_data)

testing_metabolic_data=testing_data$metabolic_data

#view the three data sets you now have

training_data
testing_data
testing_metabolic_data

set.seed(1)

#grow the tree

tree_name=rpart(metabolic_data~.,data=training_data)

#look at the tree results

tree_name
#graph the tree using the partykit package you already loaded

plot(as.party(tree_name),tp_args=list(id=FALSE))

#now you want to check the accuracy of your tree using the testing data
("tree_pred" is what your predicted y-variables will be called; "mean" returns the
misclassification error using the predicted values (tree_pred) and the actual
values (testing_metabolic_data); "class" because this is a classification tree (i.e.
not regression)).

tree_pred=predict(tree_name,testing_data,type="class")
mean(tree_pred != testing_metabolic_data)

#cptable element of rpart object tells us whether the tree should be pruned:

print(tree_name$cptable)
```

#we want to look at "xerror", smaller is better. We want to use the number of splits having the smallest error

#prune tree (enter whatever cp you want to prune at)

pruned_tree=prune(tree_name,cp=0.04)

#plot pruned tree

plot(as.party(pruned_tree),tp_args=list(id=FALSE))

#check the pruned tree for accuracy using the testing data. "mean" will return the misclassification error, which now should be lower than the previous error you calculated, but may not be in all cases (pruning doesn't always work)

tree_pred2=predict(pruned_tree,testing_data,type="class")
mean(tree_pred2 != testing_metabolic_data)

##

A10. Copyright permissions.
##

copyright permissions for thesis

Nickolas Kosmenko <kosmenk@uwindsor.ca>

Aug 19 (5 days ago)

to Tim, Ken, Christina

Hi Tim, Ken, and Tina,

I received my thesis back from grad studies with their formatting comments. One of the comments (pertaining to the declaration of co-authorship page) was:

"Pleae email your supervisors asking them (or who ever was involved in the publication "in preparation" and ask for their permission to use the material in your thesis. The email with your equest and their answers should be added as an Appendix at the end. If you have questions, please come in for discussion."

Could I please get these permissions from you to include in my appendices section?

Thanks,
Nick

Christina Semeniuk <semeniuk@uwindsor.ca> Aug 19 (5 days ago)

to me, Tim, Kenneth

Hi Nick - you have my permission.

Regards,

Tina

On 2015-08-19, at 10:07 AM, Nickolas Kosmenko <kosmenk@uwindsor.ca<mailto:kosmenk@uwindsor.ca>>

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Kenneth Drouillard <kgd@uwindsor.ca>   Aug 19 (5 days ago)

 to me

Nick you have my permission to use materials utilized in chapters 2 and 3 as part of your thesis.

From: Nickolas Kosmenko [mailto:kosmenk@uwindsor.ca]
Sent: Wednesday, August 19, 2015 10:07 AM
To: Johnson, Tim (MNR) <tim.johnson@ontario.ca>; Kenneth Drouillard <kgd@uwindsor.ca>; Christina Semeniuk <semeniuk@uwindsor.ca>
Subject: copyright permissions for thesis

Johnson, Tim (MNRF) <tim.johnson@ontario.ca> 9:45 AM (6 minutes ago)

 to me, Ken, Christina

Nick,

As you thesis co-supervisor and a co-author on publications related to your research, I give you

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permission to use the data and results pertaining to the research in your thesis.

Tim

****
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