The Energetic Consequences Of Winter Foraging For Northern Temperate Fish Species

Benjamin David Block
University of Vermont

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THE ENERGETIC CONSEQUENCES OF WINTER FORAGING FOR NORTHERN TEMPERATE FISH SPECIES

A Thesis Presented

by

Benjamin D. Block

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Biology

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Thesis Examination Committee:

Jason D. Stockwell, Ph.D., Advisor
J. Ellen Marsden, Ph.D., Advisor
Jana Kraft, Ph.D., Chairperson
Cynthia J. Forehand, Ph.D., Dean of the Graduate College
Abstract

The seasonal energy dynamics of temperate fishes will likely be affected by climate change, especially during the winter. To date, freshwater fish are understudied in winter compared to other aquatic organisms, and additional winter-focused studies are urgently needed. Recent research has demonstrated that some fish species are more active in winter than previously thought, therefore, an inquiry into the energetic contributions of winter foraging to the annual growth of freshwater fishes is needed prior to imminent changes in winter conditions. Here I have empirically shown that winter foraging behavior and seasonal energy dynamics likely depend on the thermal preference of individual fish species. I compared the seasonal energy dynamics of the cool-water species yellow perch (*Perca flavescens*) to two warm-water species, pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*). Our results support our first hypothesis that cool-water species should forage in all seasons whereas warm-water species forage in the open-water seasons but exhibit reduced foraging in the winter. Our results also support our second hypothesis that winter foraging provides sufficient energy for overwinter growth in cool-water species but does not provide sufficient energy for overwinter growth in warm-water species. The relationships between winter foraging and seasonal energy dynamics of these fishes will likely be altered due to climate change. Decreased ice cover duration and increases in water temperatures and ambient light will likely affect the seasonal energy dynamics that these species have evolved to tolerate winter conditions in temperate lakes. Thus, changes to the seasonal energy dynamics of fishes would not only affect individual survival and reproductive success but also the transfer of energy through food webs, and recreational and commercial fisheries.
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CHAPTER 1: LITERATURE REVIEW

Introduction

The seasonal energy dynamics of temperate fishes will likely be affected by climate change, especially during the winter (Hurst 2007; Shuter et al. 2012; Dokulil et al. 2014). Unfortunately, winter is the most understudied season in fisheries ecology, often due to the logistical challenges of winter fieldwork (Fernandes and McMeans 2019). Nevertheless, the causal relationships between current winter conditions and the seasonal energy dynamics of fish must be elucidated before any future climate change predictions can be made.

Temperate lakes in winter are characterized by low water temperatures and low light conditions (Gates 1962; Bertilsson et al. 2013; Hampton et al. 2017). Others have also characterized winter in small lakes or bays of larger lakes as the period between ice formation and ice melt (Block et al. 2019; Knoll et al. 2019; Sharma et al. 2019). Water temperatures in winter range between 0 and 4°C and the under-ice period is thought to be characterized by a pattern of inverse thermal stratification, with the coldest water just below the ice and the warmest, most dense water near the bottom (Wetzel 2001). High-frequency buoy data from Lake Sunapee, NH, however, suggests that inverse stratification may be a more dynamic process than previously thought and, with climate change, may cease entirely (Bruesewitz et al. 2015). Light levels in winter are reduced compared to summer because of the decreases in solar radiation and the angle at which solar radiation strikes the Earth (Gates 1962). Snow cover can also significantly reduce light penetrations, whereas clear ice has a negligible effect (Bertilsson et al. 2013; Block
et al. 2019). Ice and snow cover also produce an albedo effect that reflects solar radiation and further limits light penetration into lakes (Austin and Colman 2007).

Fish are obligate poikilotherms, and therefore, their internal body temperatures closely mirror ambient water temperatures (Magnuson et al. 1979; Hasnain et al. 2010; Hatton et al. 2018). Low winter water temperatures result in a suite of physiological changes that affect fish across multiple scales from organismal to cellular processes, including behavior, brain function, neural processes, cell membrane fluidity, and enzymatic activity (Suski and Ridgeway 2009). Consumption, digestion, and metabolic rates are positively correlated with temperature, and thus slower in winter (Clarke and Johnston 1999; Barneche and Allen 2018). Low light levels, as a result of low sun angle as well as snow and ice cover, can limit visual predation, induce behavioral changes, and further suppress biochemical reaction rates (Jacobsen et al. 2002; Speers-Roesch et al. 2018). Therefore, winter conditions produce physiological changes in fish that can have energetic repercussions in individuals.

Fish exhibit a variety of strategies to mitigate the energetic demands of winter to maximize stored energy and body condition. Prior to winter, spring-spawning fish accumulate and store energy for winter in the form of lipids, whereas fall-spawning fish release large amounts of energy, in the form of gametes, and enter winter with low energy reserves (Newsome and Leduc 1975). All species possess behavioral adaptations that reduce metabolic activity and subsequent depletion of winter energy reserves (Speers-Roesch et al. 2018). Consequently, certain fishes forgo feeding in winter and rely solely on energy reserves to survive, while other species are able to forage and obtain a
net energy gain in the winter (Klemetsen et al. 2003; Shuter et al. 2012; Stockwell et al. 2014). Thus, the winter plays an integral role in the seasonal energy dynamics of temperate fishes.

Winter lake conditions (i.e., low water temperatures and ice cover) are likely to change due to global climate warming (Magnuson et al. 2000). Decreases in seasonal ice cover duration will likely influence all biota from microbes to fish (Gerten and Adrian 2000; Bertilsson et al. 2013; Carey and Zimmerman 2014). Although longer “growing seasons” are predicted to increase fish growth, changes in winter conditions may affect reproductive success and effectively negate increased growth (Magnuson et al. 1997; Farmer et al. 2015). Mechanisms that fish have evolved to endure winter conditions will be affected by predicted higher water temperatures and higher light levels (Kirillin 2010; Poesch et al. 2016; Woolway and Merchant 2019). Metabolic rates are higher at warmer temperatures; therefore, rates of energy depletion will increase in winters with warmer water temperatures (Clarke and Johnston 1999; Barneche and Allen 2018; Hewitt et al. 2018). Increased light levels can increase foraging success by visual predators but may also increase metabolic rates, even in winter inactive fish (Jacobsen et al. 2002; Speers-Roesch et al. 2018). Thus, as climate change progresses, warmer winters may be more energetically costly for temperate fishes. Population growth and the transfer of energy through food webs will also be affected (Farmer et al. 2015; Barneche and Allen 2018).

The objectives of this review are to review the various strategies that fish use to conserve energy during the winter in fresh water, primarily lakes, at latitudes where ice cover is expected to occur. In addition, we will identify how winter energy dynamics of fish
contribute to individual and population growth, and how climate change will affect these relationships.

**Methods**

I used Web of Science to search the published literature on the winter ecology of freshwater fishes in lakes and rivers in north temperate regions. All publication years were included. The purpose of the systematic literature search was to determine the number of studies focused on the winter ecology of cool- and warm-water fishes as opposed to studies focused on cold-water fishes. Results from my search highlight the paucity of studies that have focused on winter fish ecology (Table 1.1).

A large number of papers focused on cold-water species (n= 53/118), most of which were salmonid species. Similarly, of field-studies found, 72% (n= 35/52) were on cold-water species. What is glaringly obvious is the lack of primary literature that focuses on cool- and warm-water species, especially field-studies. Fernandes and McMeans (2019), in their review of winter energy storage strategies, found similar results and noted that more research on cool- and warm-water species in winter is desperately needed.

**Definition of winter**

Winter is the season between ice formation and ice melt in northern temperate lakes (Block et al. 2019; Knoll et al. 2019; Sharma et al. 2019). In large lakes and river systems with infrequent ice cover, winter can also be characterized by low water temperatures and low light conditions (Gates 1962; Bertilsson et al. 2013; Hampton et al. 2017). Ice-on and ice-off dates can vary spatially within a large system, therefore winter duration should be defined for the location of observation and not necessarily for the entire system.
The duration of winter, determined by ice cover duration, changes with altitude, latitude, and proximity to oceans.

**The abiotic and biotic conditions of winter and their effects on fish physiology**

**Winter conditions**

In winter, water temperatures decrease to annual lows due to decreases in solar radiation and the angle at which solar radiation strikes the Earth (Gates 1962). The amount of solar radiation that strikes the earth in winter decreases at higher latitudes; therefore, lakes at higher latitudes have longer winter periods (e.g., Eloranta et al. 2013a). Ice cover formation is largely dependent on the winter air temperature but also is affected by latitude, lake volume, wind velocity, and fetch (Shuter et al. 1983). Lakes can have sporadic ice cover, with frequent forming and melting events, or can be consistently frozen for the entire winter (Weyhenmeyer et al. 2011; Edlund et al. 2017; Hewitt et al. 2018). Clear ice has a minimal effect on light attenuation; however, snow and opaque ice significantly affect light penetration (Bolsenga and Vanderploeg 1992; Bertilsson et al. 2013). Ice cover prevents atmospheric inputs of particulate matter, prevents heat loss to the atmosphere, limits gas exchange, and determines lake warming and stratification processes in spring and summer (Livingstone 1997; O’Reilly et al. 2015; Hewitt et al. 2018). Once ice forms, an ice-albedo effect causes solar radiation to be reflected back into the atmosphere and further limits solar warming in winter. Ice-albedo effects have profound effects on annual water temperature dynamics (Austin and Colman 2007). Snow depth strongly limits photosynthetically active radiation and limits under-ice primary production (Pernica et al. 2017). In productive systems, water beneath the ice can
become anoxic and lead to fish kills (Magnuson 2010). Thus, ice phenology, or changes in the duration and physical properties of ice cover, can directly be affected by climate and be used to assess climate change impacts on freshwater food webs (Magnuson et al. 2000; Adrian et al. 2009; Weyhenmeyer et al. 2011).

Light limitation beneath the ice varies in time and space within a lake due to ice thickness and the patchiness of wind-blown snow. Many freshwater fishes are visual predators and foraging can be hindered by light limitation in winter (e.g., Jacobsen et al. 2002). In lakes with high primary production or suspended materials in summer, higher light attenuation in summer may cause fish to be able to visually orient themselves better in winter than in summer (e.g., Hergenrader and Hasler 1968). Conversely, fishes that inhabit dystrophic, humic lakes may be visually limited in winter (Hedström et al. 2017).

*Physiological challenges of winter*

The physiological abilities of fish strongly depend on ambient water temperatures (Magnuson et al. 1979). Species evolve to perform optimally within a given temperature range. The temperature range for optimal growth is of particular importance to population growth and the flow of energy through ecosystems (Pörtner 2010; Shuter et al. 2012; Barneche and Allen 2018). Freshwater fishes are often categorized by their optimal temperature range into three thermal guilds: cold-water (< 19°C), cool-water (19°C - 25°C), and warm-water (> 25°C) species (Magnuson et al. 1979; Hasnain et al. 2010, 2013). Most freshwater fish species perform optimally at water temperatures higher than winter temperatures (0 - 4°C).
Ambient water temperatures below optimal water temperatures cause a suite of physiological changes that can significantly impact the seasonal energy dynamics and growth of fish. Digestion and metabolic rates decrease drastically at sub-optimal temperatures for most freshwater species (Randall et al. 1997) except winter-specialists such as burbot \textit{Lota lota} (Hölker et al. 2004; Harrison et al. 2016; Grabowski et al. 2020). Similarly, oxygen consumption and the scope for activity are lowest at low water temperatures (Beamish 1970; Clarke and Fraser 2004). The activity of enzymes, ion pumps, and ion channels are slowed (Hochachka 1988; Somero 1995). Also, low water temperatures reduce the fluidity of cellular membranes and decrease eye and brain function in most freshwater fishes (Hazel 1984).

Cellular temperature compensation allows fish to maintain high metabolic capabilities at cold temperatures and involves increased aerobic muscle mass, red muscle mass, and heart ventricle mass (Roots and Prosser 1962; Kolok 1991). An increased heart somatic index is thought to maintain swimming capacity at cold temperatures (Driedzic et al. 1996). These compensations have been primarily found in winter-active fishes that can afford high metabolic rates (Ultsch 1989). For winter-inactive fishes, that rely on low metabolic rates to survive winter, the literature shows confounding views on whether temperature compensation occurs (Ultsch 1989; Kolok 1991; Sephton and Driedzc 1991). The ability to sustain high metabolic rates at cold temperatures is surely a luxury expense that only species that have high energy stores or feed in winter are able to afford.
Bioenergetics of winter on energy allocation

Fish use energy obtained from feeding for metabolism, somatic growth, reproduction, and, if in excess, store energy for later use. Metabolic costs, prey abundance, foraging success, and predator avoidance can affect the energy dynamics of fish (Byström et al. 2006; Eloranta et al. 2013). In winter, when conditions are often suboptimal, energy dynamics must be optimized to ensure individual survival and, in spring-spawning fish, the maturation of gonads (Shuter et al. 2012). In spring-spawning fish, the depletion of energy stores in winter can cause individuals with low energy reserves to be more prone to mortality and more likely to forgo spawning (Henderson and Nepszy 1994; Biro et al. 2004). Thus, factors that directly affect the seasonal energy dynamics of fish can directly affect individual survival and reproductive success.

Fitness can be assessed through a bioenergetics framework. A bioenergetics framework can be used to evaluate how fish consume and allocate energy throughout the year. Ingested energy from prey is allocated into major physiological components and described using an energy budget equation (Jobling 1994):

\[ C = (R + A + SDA) + (F + U) + G \]

where \( C \) = consumption, \( R \) = standard metabolism, \( A \) = energy expenditure due to activity, \( SDA \) = specific dynamic action (energy required to digest food), \( F \) = egestion, \( U \) = excretion, and \( G \) = growth. Growth can further be broken down into three subunits:

\[ G = G_{somatic} + G_{gonadal} + G_{storage} \]
where energy consumed is allocated either to somatic growth \((G_{\text{somatic}})\), gonadal growth \((G_{\text{gonadal}})\), or stored for future use \((G_{\text{storage}})\), usually as lipids.

The second law of thermodynamics states that the energy budget must always balance because energy can neither be created nor destroyed. The four components of the energy model: maintenance, somatic growth, reproductive growth, and energy storage, can be compared among one another and used to evaluate individual fitness (Figure 2). Energy allocated to tissue maintenance increases survival potential because poor condition and low energy reserves increase the risk of disease or death (Finstad et al. 2004a). Energy allocated to somatic growth increases fish size, fecundity, and foraging success, and reduces predation risks, and thus, increases the likelihood of future reproductive success (Peters 1983). Energy allocated to reproductive growth immediately increases short-term reproductive success and fitness. Energy reserved for future use allows fish to survive adverse periods when energy consumption is limited. Also, reproduction based on energy reserves (‘capital breeding’) is an adaptive strategy that many ectotherms, including fish, use to reproduce in a time period that maximizes fitness (Ejsmond et al. 2015). Energy stored for future use does, however, constrain immediate growth. The ‘Total Switching Strategy’ is where all assimilated energy is applied to somatic growth during the first part of the growing season and then, at some point, all assimilated energy is applied to storage growth (Giacomini and Shuter 2013). Consequently, trade-offs between building energy reserves and immediate growth have the potential to impact fitness. The mechanisms that determine how energy is allocated in winter are of particular interest because of the
multitude of abiotic and biotic constraints imposed on fish and the potential effects on individual and population growth.

The energetics of overwintering

Fish, and all other animals, store energy for later use in the form of lipids, which are stored in visceral fat but also in adipose tissue (Tocher et al. 2003; Fernandes and McMeans 2019). Lipid reserves allow fish to store energy in a season of abundant food and catabolize stored energy in seasons with less food availability (Ultsch 1989; Giacomini and Shuter 2013). In winter, the energy dynamics of fish depend on whether a species actively forages. Winter foraging subsidizes energy reserves and can be used for maintenance or growth (Shuter et al. 2012). If a species ceases foraging in winter, energy reserves must be sufficiently large for overwinter survival, and in the case of mature individuals, successful reproduction (Henderson and Nepszy 1994). Some warm-water fish, however, spawn months after ice-out and may use energy consumed between winter and spawning for gonadal development. Thus, somatic and reproductive growth potentials are dependent on lipid reserves prior to winter and the depletion rate of lipid stores over the winter.

Energy storage

The extent of pre-winter energy reserves are species- and individual-specific and are dependent on successful energy consumption. The depletion rates of energy reserves are largely affected by overwinter metabolic rates, especially in species that do not actively forage in winter. Yellow perch *Perca flavescens* starve under simulated winter conditions
and survive on energy reserves for nearly seven months, due to their low metabolic rates (Newsome and Leduc 1975). Winter feeding likely would have extended the survival period (Shuter et al. 2012). Overwinter energy reserves can be affected by migration, reproduction, and body size (Henderson and Nepszy 1994; Biro et al. 2004; Byström et al. 2006; Bronmark et al. 2008). Energy reserves and depletion rates are also dependent on winter duration, which is correlated with latitude (Giacomini and Shuter 2013).

Populations at higher latitudes can experience significantly longer winters that require larger energy reserves to meet the energetic demands of winter than lower latitude populations. The sizes of pre-winter lipid reserves of young-of-the-year (YOY) Atlantic salmon *Salmo salar* increase with increasing latitude and ice cover duration (Berg et al. 2009). High-latitude Atlantic salmon populations experience a longer winter than low-latitude populations and adjust their feeding behavior to prepare a sufficient energy reserve prior to winter (Finstad et al. 2010). A latitudinal gradient in lipid storage and depletion was also observed in Atlantic silversides *Menidia menidia* (Schultz and Conover 1997). Thus, populations of the same species demonstrate differences in pre-winter feeding behavior and energy storage along a latitudinal gradient.

Pre-winter lipid reserves are also dependent on the reproductive life history of a species and whether individuals are reproductively mature. Spring-spawning fish require surplus energy to successfully spawn in spring and survive thereafter (Henderson and Nepszy 1994). Surplus energy is excess stored energy beyond that which is needed for overwinter metabolic demands and the energy needed to mature gonads. Walleye *Sander vitreus* do not spawn if surplus energy is not obtained prior to spawning in the spring (Henderson
and Nepszy 1994). Reproductive maturity can account for individual variations in pre-winter energy reserves. Reproductive females store more lipids prior to winter than non-reproductive females (Reznick and Braun 1987). However, unlike spring-spawning fish, many cold-water fishes spawn in fall and consume energy that is used to repair and maintain tissues (Amundsen and Knudsen 2009; Shuter et al. 2012). The sizes of energy reserves in winter vary by species, maturity, and the timing of spawning.

The extent of energy reserves in winter are also dependent on the body size of fish. Variation in annual lipid cycling decreases as body size increases and explains intraspecies and interspecies variation of lipid levels in winter (Fernandes and McMeans 2019). The relationship between body size, the size of pre-winter energy stores, and differential overwinter survival has been demonstrated in YOY European perch *Perca fluviatlis* (Heermann et al. 2009). Larger adult bluegills *Lepomis macrochirus* emerge from winter with higher energy stores than do smaller adults, further supporting the idea that pre-winter energy reserves are positively related to body size (Cargnelli and Gross 1997). Conversely, a laboratory experiment found that large age-0 rainbow trout *Oncorhynchus mykiss* had smaller percent total lipid stores at the end of winter than smaller conspecifics, likely due to limited food availability (Connolly and Petersen 2003). Overwinter survival of YOY Pacific herring *Clupea pallasi* is dependent on the amount of energy stored before winter (Foy et al. 1999). Size-dependent mortality risks lead to different overwinter foraging strategies for different size classes of walleye pollock *Theragra chalcogramma*. Young-of-year walleye pollock have a high overwinter starvation risk, presumably due to small pre-winter energy reserves, and thus actively
foraged in winter while age-1+ juveniles relied on pre-winter energy reserves for overwinter survival and minimized overwinter foraging (Heintz and Vollenweider 2010). The relationship between body size and lipid content clearly supports the critical size hypothesis – individuals must be of sufficient size in their first year of life to successfully survive their first winter and be recruited into a population (Beamish and Mahnken 2001; Hurst 2007).

**Behavioral adaptations for decreasing energy demand in winter**

Although the energetic demands of winter can be met with sufficiently large pre-winter energy reserves, fish also exhibit overwinter behaviors that reduce energetic costs and reduce energy depletion rates (Ultsch 1989; Binner et al. 2008). Freshwater fishes can be classified into two winter survival strategies: winter-active and winter-inactive, each of which behaviorally reduces the energetic cost of overwintering (Shuter et al. 2012). Winter-inactive fish cease foraging, rely on energy reserves, and reduce metabolic costs by remaining in sheltered habitats – habitats that reduce energy expenditure (e.g., slow-moving river sections). Conversely, winter-active fish obtain a net energy gain from winter foraging and reduce the rate of energy depletion over winter. Winter-active and winter-inactive fish respond differently to exercise at low temperatures, primarily in terms of cardiac output (Cooke et al. 2003). In addition, there are species that exhibit characteristics of both active and inactive strategies (e.g., yellow perch – Ultsch 1989; Johnson and Evans 1991), however, under what conditions an individual adheres to a particular strategy is unclear.
The metabolic rates of winter-inactive fish are reduced in winter due to decreased activity, cold water temperatures, and low light levels rather than metabolic rate depression – an active downregulation of resting cellular energy turnover (Speers-Roesch et al. 2018). Voluntary activity, from foraging to predator avoidance, has been estimated to represent up to 67% of routine metabolic rates in fish, therefore, inactivity results in energy savings (Nilsson et al. 1993). Winter water temperatures greatly dampen diel activity cycles in cunner *Tautogolabrus adspersus* such that day and night metabolic rates are similar under winter conditions. Cunner respond to acute increases in light by becoming temporarily active and increasing their metabolic rate (Speers-Roesch et al. 2018). As a result, darkness can further suppress metabolic rates during winter inactivity. Intraspecific variability in the downregulation of metabolism and activity produces variable rates of overwinter energy depletion (Schultz and Conover 1999, Biro et al. 2004, Auer et al. 2016). Metabolic rates can be expected to increase under conditions that promote warmer water temperatures and increased light penetration to lakes in winter, for example, decreased ice cover due to climate change (Kirill in 2010).

Behavioral changes that reduce overall activity are important for winter-inactive fish to conserve energy reserves. Cisco *Coregonus artedi* in Ten Mile Lake, MN, continue to feed in the winter, however, they do not exhibit diel vertical migration as they do in other seasons (Ahrenstorff and Hrabik 2016), which suggests the benefits of the behavior are either not present or are energetically too costly. Conversely, activity levels of European perch varied little seasonally; however, perch moved for shorter periods of time in the winter because of shorter day lengths (Jacobsen et al. 2002). Stream-dwelling salmonids
minimize the energetic cost of maintaining their position by moving to stream stretches with low water velocity in winter (Cunjak and Power 1986).

Winter foraging

In some older literature freshwater fish are assumed to cease foraging in the winter, especially if they are warm- or cool-water species. Several laboratory studies link cold water temperatures to inactivity (Crawshaw 1984; Lemons and Crawshaw 1985). Past research, however, has shown that many fishes, representing all thermal guilds, are shown to feed in the winter (Ultsch 1989; Shuter et al. 2012). Current literature suggests that cold-water fishes, especially salmonids, are easily capable of foraging in the winter (Eloranta et al. 2013; Hayden et al. 2013; Stockwell et al. 2014). Cool-water fishes show a similar trend (Jacobsen et al. 2002) but behaviors may vary depending on the species (Shuter et al. 2012). The literature on warm-water fishes is not as straightforward and gives examples of both foraging and non-foraging winter behaviors (Cargnelli and Gross 1997; Garvey et al. 2004). Age-0 largemouth bass *Micropterus salmoides* may forage in the winter depending on size, prey assemblage, predator abundance, water temperature, and species (Fullerton et al. 2000; Micucci et al. 2003; Garvey et al. 2004).

Seasonal omnivory and generalist feeding on asynchronous resources are adaptive strategies that can mitigate temporally variable prey densities (McMeans et al. 2015; McMeans et al. 2016). For example, European whitefish *Coregonus lavaretus* and Arctic charr *Salvelinus alpinus* (Eloranta et al. 2013, Hayden et al. 2013) shift foraging efforts to different habitats in winter than those occupied in summer. Saugeye (female walleye
Sander vitreus x male sauger S. canadensis) consumptive demand, in Ohio Reservoirs, exceeds the supply of available gizzard shad Dorosoma cepedianum prey in spring and summer, resulting in a shift to alternative prey (Denlinger et al. 2006). Seasonal dietary shifts, that include mention of winter diets, have also been observed in lake trout Salvelinus namaycush, brown trout Salmo trutta, and yellow perch (Hasler 1945; Eck and Wells 1986; Anderson et al. 2016). Winter feeding can contribute significantly to the annual energy budget of an individual (Stockwell et al. 2014) and some species will not spawn in the spring if energy stores are too depleted (Henderson and Nepszy 1994). Alternatively, feeding may only occur when energy stores decline to a threshold level that a fish must “defend” (Metcalfe and Thorpe 1992). Whether a defended energy level exists for all species is unclear. Some research suggests that winter foraging only occurs to supplement or maintain pre-winter energy reserves (Amundsen and Knudsen 2009; Finstad et al. 2010; Shuter et al. 2012). Arctic charr in Scandinavia feed during the winter on benthos as well as zooplankton; however, their body lipid content still decreases and energy gained from feeding does not exceed maintenance costs (Finstad et al. 2003; Amundsen and Knudsen 2009; Eloranta et al. 2013a). Winter feeding that did not exceed maintenance costs has also been observed in rainbow trout, Pacific herring, age-0 kokanee Oncorhynchus nerka, and European perch (Foy et al. 1999; Steinhart and Wurtsbaugh 2003; Eckmann 2004; Flinders and Magoullick 2017). Metabolic costs associated with the acclimation to rapidly declining water temperatures may explain metabolic deficits in age-0 brook trout Salvelinus fontinalis and brown trout (Cunjak and Power 1987). Why these fishes continue to feed in winter without an energetic benefit is
unclear. Winter foraging behaviors may be beneficial under certain winter conditions, but fish maintain the behaviors even if conditions are not ideal and foraging is not sufficient to meet energetic demands.

In contrast, other literature has shown that many fishes not only supplement energy stores but also can grow by feeding in the winter. Fish at colder temperatures require substantially less assimilated energy to produce a unit of biomass than fish at warmer temperatures, therefore, the cost of growth is less at cold temperatures (Barneche and Allen 2018). Thus, fish may have an energetic advantage by living in cold water, in terms of a decreased metabolic demand, compared to living in warm water (Clarke and Johnston 1999). Atlantic silversides compensate for the length of the growing season by having higher growth rates at latitudes with shorter growing seasons (Conover and Present 1990). Northern pike *Esox lucius* in Canada display limited seasonal variation in lipid content (Medford and Mackay 1978) yet feeding activity was lowest for the species during winter in Turkey (Alp et al. 2008). Small stream-dwelling brown trout grew, and the condition of larger individuals increased over winter (French et al. 2014). Ruffe *Gymnocephalus cernuus* also gained mass over the winter (Eckmann 2004), perhaps due to a sensitive lateral line system that aids foraging in complete darkness (Disler and Smirnov 1977). Winter feeding by Arctic charr in Norway was equal to energetic demands in one lake and exceeded metabolic costs in another, likely due to differences in littoral prey abundance (Klemetsen et al. 2003). Additional instances when winter foraging met or exceeded energetic demands include European perch (Sullivan 1986), bloater *Coregonus hoyi* (Rudstam et al. 1994), Arctic charr (Siikavuopio et al. 2009), and
whitefish *Coregonus lavaretus* (Tolonen 1998). Marine fishes such as polar cod *Boreogadus saida* (Lønne and Gulliksen 1989), cod *Gadus morhua* (Hop and Gjøsæter 1993), sea trout *Salmo trutta* (Rikardsen et al. 2006), Alaskan pollock *Gadus chalcogrammus* (Wilson et al. 2011), and winter flounder *Pseudopleuronectes americanus* (Bell 2012) often also obtain a net energy gain from winter feeding.

Body size dictates how much energy needs to be obtained through foraging to meet energetic demands. Small fish have high weight-specific metabolic rates which cause them to deplete energy reserves at faster rates than large fish. However, smaller individuals can sustain themselves at lower resource levels than larger individuals (Byström and Andersson 2005). The critical resource density (CRD) – the prey density at which energy intake balances metabolic demands – increases with body size (Byström et al. 2006). Therefore, large individuals, with a higher CRD, begin to starve earlier with decreasing prey densities; however, once prey densities decrease below the CRD for all size classes, small individuals would starve more quickly due to their higher metabolic rate. Winter conditions may favor small or large individuals of the same population depending on prey densities and metabolic rates. Thus, while the energetic demands of winter seem to be mitigated by sufficiently large pre-winter energy reserves, the true picture generated by the available literature remains grainy. Utsch (1989) hypothesized that fish species that need the highest pre-winter energy reserves are those that experience a long winter, do not feed in the winter, spawn in the spring, and are small compared to larger species. Conversely, fishes that feed in the winter can afford to maintain high metabolic rates and high activity because feeding supplements those additional energetic
costs. Regardless of winter survival strategy, these behaviors may be subject to immense changes due to decreased winter severity and duration.

**Climate change and its effects on winter fish ecology**

Climate change is likely to change abiotic and biotic conditions in lakes (Williamson et al. 2009). Lake processes and biota will be affected in a variety of ways due to changes in temperature, wind, and precipitation (O’Reilly et al. 2015; Poesch et al. 2016; Woolway and Merchant 2019). Northern lakes that have a winter season are to experience stronger stratification in summer, longer ice-free seasons, warmer winters, and decreased ice thickness (Edlund et al. 2017). Ice cover duration has steadily decreased over the last two centuries (Magnuson et al. 2000) and at some point, in the future, many temperate lakes will no longer have an ice-covered period (Weyhenmeyer et al. 2011). Models have predicted that warmer spring and winter air temperatures contribute to earlier ice-off while warmer temperatures in fall delay ice-on. In the Laurentian Great Lakes region, ice-on is projected to be delayed by 11 days and ice-off is projected to be 13 days earlier on average by 2070 (Hewitt et al. 2018). Similar trends are occurring globally (Magnuson et al. 2000; Kirillin 2010; Woolway and Merchant 2019). Decreases in ice cover duration and ice thickness will affect under-ice light penetration, mixing regimes, and the seasonal energy dynamics of fish.

Climate change will directly affect the bioenergetics of fishes in winter due to changes in light levels, water temperature, ice cover, and prey availability. Darkness promotes decreases in metabolic rates during winter inactivity (Speers-Roesch et al. 2018), thus, metabolic rates would be expected to increase under conditions that promote higher light
levels. Decreased ice cover may also have negative effects on fish production by decreasing the energetic status and shrinking available habitat of stream-dwelling fish during winter (Watz et al. 2016). Conversely, fish would be able to forage more efficiently or for a longer period, because of increased light without ice cover, than when lakes are ice-covered (Jacobsen et al. 2002).

Warmer water temperatures in winter will increase metabolic rates of fishes and affect growth if fish are unable to behaviorally thermoregulate themselves or expand their range poleward (Shuter and Post 1990; Clarke and Johnston 1999; Sharma et al. 2007; Farmer et al. 2015; Kao et al. 2015). Higher metabolic demand in the winter may in turn limit spring reproductive success if a significant portion of an individual’s surplus energy is depleted. Depleted surplus energy can cause low-quality spawning events, weak year-class strength, and translate into decreased population size and fish production. Following warm winters, Lake Erie yellow perch produce smaller eggs that hatched at lower rates and produce smaller larvae than perch that spawned following cold winters (Farmer et al. 2015). Warmer winter temperatures may be beneficial in some systems and detrimental in others. Production of least cisco Coregonus sardinella in Arctic Alaskan lakes is projected to increase with warmer water temperatures if feeding rates remain constant (Carey and Zimmerman 2014). Salmonids in warm streams currently cooled by snowmelt will grow less while fish in sub-optimally cool streams will grow more (Beer and Anderson 2013). Walleye in a Kansas reservoir are predicted to lose up to 65% of their body mass during the summer if water temperature increases by 10%; whereas growth during fall, winter, and spring may increase up to 150% (Quist et al. 2002). In addition to
increased water temperatures, the effect of resource availability on the overwinter survival of fishes should be considered (Brodersen et al. 2011). Winter assemblages of phytoplankton and zooplankton will be affected by climate change (Dokulil and Herzig 2009). The frequency of winter fish kills will decrease in the future because of more oxygenated waters, and therefore, predator-prey interactions between fish and zooplankton are likely to have cascading effects on other trophic levels (Balayla et al. 2010). The effects of climate change on predator energy demands may increase predation pressure on prey populations. Changes in the timing of predator-prey interactions may lead to shifts in food web dynamics (Breeggemann et al. 2016). If metabolism increases at a rate that is not matched by increased energy consumption, then less assimilated energy is available for growth. Ultimately, the effects of climate change will disrupt lake systems and directly affect the bioenergetics of fishes.

**Conclusion**

Ectothermic fish are significantly affected by seasonal changes in their environment, specifically, fish behaviorally and metabolically respond directly to changes in water temperature and ambient light levels. In winter, low water temperatures cause physiological effects in fish that do not occur in open-water seasons. In addition, light penetration decreases significantly in winter which limits many behaviors reliant on vision. Changes in the behavior and physiology of fish directly affect energy consumption and allocation, therefore, the abiotic conditions of winter directly influence the seasonal energy dynamics of fish.
The amount of energy needed to meet the energetic demands of winter is dependent on many factors. Active winter foraging boosts energy reserves accumulated prior to winter. Latitude and winter severity and duration determine the energy content needed to survive. Also, the size of energy reserves varies with reproductive life histories, maturity, and body size. Fish can reduce the energetic demand of winter by ceasing all activities that do not promote a net-positive energy balance. Whether winter feeding is energetically beneficial likely depends on prey energy density, the amount of food ingested, digestion and metabolic rates associated with foraging, body size, and winter severity. A clear trend in which abiotic and biotic conditions make winter foraging beneficial to individual growth has not been found.

A thorough comprehension of fish bioenergetics in winter is needed, especially in the face of existing climate change. Current trends of continually decreasing ice cover duration will reach a point at which most temperate lakes will no longer have an ice-covered season. Changes in ice phenology will directly affect fishes through changes in light penetration, water temperature, prey availability, and metabolic responses. Climate change may disrupt or destroy under-ice subsistence and recreational fisheries, impact fish production, and affect energy flow through ecosystems (Moulton et al. 2010, Barneche and Allen 2018). Ultimately, the seasonal energy dynamics of fishes must include winter research and be directly applicable to conservation efforts of fish that inhabit seasonally ice-covered lakes.
References


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Tables and Figures

Table 1.1: Results of literature searches using Web of Science academic search engine to locate reference materials. Search strings that include quotation marks indicate that the exact phrasing needed to be within the literature itself. Search strings without quotations often resulted in too many results.

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Fig. 1.1: Amount of solar radiation received on a horizontal surface for different latitudes at different months of the year. Latitude is presented at 10° intervals. The figure was taken from Suski and Ridgeway (2009), Blackwell Publishing Ltd. Figure originally taken from Wetzel (1983), Elsevier (Harcourt Publishers).
Fig. 1.2: The pattern of energy allocation in individual fish. Costs at each step are shown on the left and the remaining energy is further allocated. The figure was taken from Wootton (2011).
CHAPTER 2: CONTRIBUTIONS OF WINTER FORAGING TO THE ANNUAL GROWTH OF THERMALLY DISSIMILAR FISH SPECIES

Abstract

The seasonal energy dynamics of temperate fishes will likely be affected by climate change, especially during the winter due to changes in ice phenology; however, few studies have focused on this season. Recent research has shown that some fishes are more active in winter than previously thought, thus, an inquiry into the energetic contributions of winter foraging to the annual growth of fishes is needed prior to imminent changes in winter ice phenology. We used fish demographic data, stomach content data, percent total lipid analyses, and bioenergetics modeling to assess the effects of winter foraging on the seasonal energy dynamics of three fish species in Lake Champlain, VT. We compared the seasonal energy dynamics of species in two thermal guilds, the cool-water species yellow perch (*Perca flavescens*) and two warm-water species, pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*). The data suggest that winter foraging behavior and seasonal energy dynamics likely depend on the thermal preference of individual fish species. Our results indicate that cool-water species can forage in all seasons whereas warm-water species forage in the open-water seasons but do not forage in winter. Bioenergetic modeling showed that winter foraging provides sufficient energy for overwinter growth in cool-water species but does not in warm-water species. Climate change will affect the seasonal energy dynamics that these species have evolved to tolerate winter conditions in temperate lakes. Thus, changes to the seasonal energy dynamics of fishes may affect individual survival and reproductive success.
Introduction

Winter is logistically challenging for fieldwork in temperate freshwater lakes. Consequently, few studies have focused on winter (Salonen et al. 2009; Hampton et al. 2015; Hampton et al. 2017), and those that have been done mostly studied lake physics, ice phenology, water chemistry, and plankton (Weyhenmeyer et al. 2011; Bertilsson et al. 2013; Hampton et al. 2017; Mariash et al. 2017). To date, freshwater fish have been understudied in winter (Salonen et al. 2009; Shuter et al. 2012; Fernandes and McMeans 2019); however, winter conditions have the potential to affect species coexistence within systems, fish maternal condition, energy allocation, reproductive success, and recruitment (Farmer et al. 2015; Feiner et al. 2016a, 2016b; McMeans et al. 2019). Recent research indicates that fish species are more active in winter than previously thought, and forage under low water temperatures and low light conditions (Klemetsen et al. 2003; Eloranta et al. 2013; Hayden et al. 2013). In fact, some species may consume large proportions of their yearly energy requirements during winter (Klemetsen et al. 2003; Eckmann 2004; French et al. 2014; Stockwell et al. 2014). Additional winter-focused studies are urgently needed prior to imminent climate change effects on winter conditions (Magnuson et al. 2000; Williamson et al. 2009; Christensen et al. 2013; Edlund et al. 2017). Warmer winter air temperatures and decreased ice cover durations have the potential to not only affect maternal condition, egg quality and size, reproductive success, and fitness, but also species coexistence within systems, ecosystem services, and economic growth (Magnuson et al. 2014; Orru et al. 2014: Farmer et al. 2015; Feiner et al. 2016a, 2016b; McMeans et al. 2019). While these findings are compelling developments that further our
understanding of winter fish ecology, an inquiry into the energetic contributions of winter foraging to the annual growth of freshwater fishes is needed prior to imminent changes in winter ice phenology (Magnuson et al. 2000).

Northern temperate lakes in winter are characterized by low water temperatures and low light conditions (Gates 1962; Bertilsson et al. 2013; Hampton et al. 2017). Winter in small lakes or bays of larger lakes can also be defined as the period between ice formation and ice melt (Block et al. 2019; Knoll et al. 2019; Sharma et al. 2019). Decreased solar radiation due to low sun angle in winter months limits the amount of heat and light that enter a lake; therefore, water temperatures typically range from 0 to 4°C and surface waters often freeze. Ice and snow cover produce an albedo effect that further limits light penetration (Bolsenga and Vanderploeg 1992; Austin and Colman 2007; Hrycik and Stockwell 2019).

Freshwater fish are obligate poikilotherms - their internal body temperatures closely mirror ambient water temperatures (Magnuson et al. 1979; Hasnain et al. 2010; Hatton et al. 2018). Low water temperatures are associated with a variety of physiological responses in fish, including reduced metabolic, foraging, and digestion rates, as well as behavioral changes such as reduced movement and shifts in habitat use (Beamish 1970; Somero 1995; Clarke and Fraser 2004; Suski and Ridgeway 2009). Low light conditions can further suppress chemical reaction rates and induce behavioral changes (Campbell et al. 2008; Madsen et al. 2013; Speers-Roesch et al. 2018). Many temperate fishes rely on sight to find prey; however, under ice cover, visual predation may be limited to fewer
hours during the day or eliminated entirely (Miner and Stein 1996; Vogel and Beauchamp 1999; Jacobsen et al. 2002; Keyler et al. 2019).

The degree to which winter conditions affect the foraging behavior and physiology of fish may depend on thermal preferences (Shuter et al. 2012). Fish have enzymatic and physiological specializations that allow them to grow and function optimally within a certain temperature range (Fry 1971; Magnuson et al. 1979; Hasnain et al. 2010; Hasnain et al. 2013; Chezik et al. 2014). However, physiological changes occur when water temperatures are suboptimal to thermal requirements. For example, warm-water fish (preferred temperatures >25°C) are unlikely to forage in winter because temperatures are far below their preferred range. Inactive species are unlikely to consume prey or gain energy during the winter and may exhibit a negative energy budget. Lower energy consumption and smaller energy reserves result in less energy available for reproduction (Henderson and Nepszy 1994; Giacomini and Shuter 2013; Ejsmond et al. 2015; McBride et al. 2015). Conversely, cold-water fish (preferred temperatures < 19°C) likely forage in winter because water temperatures are less likely to hinder foraging. Metabolic costs are lower in winter than in other seasons (Clarke and Johnston 1999; Barneche and Allen 2018); therefore, winter foraging may be energetically favorable because more assimilated energy could be directed towards growth, reproduction, or storage. However, growth rates are also reduced in winter (Dunlop and Shuter 2006; Shuter et al. 2012; but see Siikavuopio et al. 2009). For example, juvenile lake trout Salvelinus namaycush in Lake Champlain grow in length and sustain their body condition over winter (Wilkins 2019). Lake whitefish Coregonus clupeaformis in Lake Superior consume cisco C. artedi
eggs, which represents 34% of their annual energy consumption, and increase lipid
content over winter (Stockwell et al. 2014). Cool-water fishes (preferred temperatures 19-
25°C) may remain inactive or actively forage during the winter (Shuter et al. 2012), but
the conditions under which cool-water fishes do or do not forage are unknown. The
relationships between thermal preferences and the ability to forage in winter stem largely
from lab-based studies but a limited number of in situ studies have tested these
relationships (Shuter et al. 2012; Fernandes and McMeans 2019). Nevertheless, the
ability to forage in winter directly affects the seasonal energy dynamics, annual growth,
and reproduction of temperate fishes (Biro et al. 2004; Byström et al. 2006; Shuter et al.
2012; Eloranta et al. 2013).

Fish that forage in winter may have seasonally dissimilar diets. For example, the dietary
niches of European whitefish Coregonus lavaretus and Arctic charr Salvelinus alpinus
changed between summer and winter and were related to changes in prey resources
densities (Eloranta et al. 2013; Hayden et al. 2013). Unique winter diets, dissimilar to
summer diets, have also been observed in lake trout, brown trout Salmo trutta, and
yellow perch Perca flavescens (Hasler 1945; Eck and Wells 1986; Anderson et al. 2016).
Most research on winter diets, however, have focused on cold-water species and few
studies outside of laboratory experiments have focused on cool-water or warm-water
species. Seasonal diet differences may be due to seasonal changes in the abundance or
distribution of the forage base, physiological or behavioral changes that cause predators
to occupy different lake habitats, or changes in predator foraging strategies (Amundsen
In this study, we tested whether thermal preference determined how winter foraging contributed to the seasonal energy dynamics and growth of fish. Pumpkinseed *Lepomis gibbosus* and bluegill *L. macrochirus* (collectively “sunfish”) are warm-water species and yellow perch is a cool-water species (Hasnain et al. 2010). Cold-water fish were not investigated in the present study because of logistical challenges. We hypothesized that yellow perch forage in all seasons whereas sunfish forage in the open-water seasons but do not forage in the winter. We also hypothesized that winter foraging provides sufficient energy to exceed maintenance costs and support growth over winter in yellow perch, and a lack of winter foraging causes a depletion in overwinter energy reserves in sunfish. We tested these hypotheses in Lake Champlain using data from fish population demographics, diet, lipid content, and bioenergetics modeling.

**Methods**

*Study system*

Lake Champlain is 193 km long and 20 km at its widest point and is situated among New York and Vermont, USA, and Quebec, Canada. Keeler Bay, our study site, is a small (470 ha), shallow (12 m max. depth) embayment on the eastern side of Grand Isle, Vermont (Fig. 2.1). Shallow areas in the bay contain thick stands of emergent and submerged vegetation and provide habitat for a variety of fish species, including spawning and nursery areas for cool- and warm-water fishes (B. Pientka, VTFWD, pers. comm). Keeler Bay has ice cover for four to five months, usually from December until April. The bay is a popular recreational fishing location both during the open-water and ice-covered seasons.
**Sample collection**

From September 2018 until October 2019 we collected fish biweekly during the winter and monthly during the open-water seasons. Sampling was conducted throughout Keeler Bay. Experimental gill nets (60-m long, four-panel mesh gill nets of 44.5-, 51-, 70-, and 76-mm stretch length) and fyke nets (1.8 m x 1.0 m, double-throated, 20-mm bar mesh, with a 13.7-m lead set towards shore) were used during the open-water seasons. Nets were set for an average of 2 hrs and maximally 3 hrs to minimize digestion and regurgitation of stomach contents (Bowen 1996). In winter, fish were angled using ice fishing rods equipped with tungsten jigs (3-4 mm; size 14-16 hooks) and small maggots as bait. In all seasons, fish were immediately put on ice in the field and later stored at -20°C.

**Laboratory processing**

Fish were thawed in the laboratory, and demographic data were recorded (total length, mass, sex, and gonad mass). Ages of fish were estimated from otoliths using the “crack-and-burn” method (Schreiner and Schram 2000). Two investigators independently estimated the age of each fish and together reached a consensus age estimate. If investigators could not reach a consensus, then an additional investigator was asked to independently age the fish. Either a final consensus was made, or the individual fish was excluded from age analyses. Fish excluded from age analysis were still included in stomach content or lipid analyses.
Stomachs were removed and stored in 95% ethanol. Contents were identified and enumerated using an Olympus SZX12 dissecting microscope (Olympus Corporation, Tokyo, Japan) interfaced with a GTCO CalComp digitizer for measurements (Turning Technologies, Inc., Youngstown, Ohio, USA). Prey taxa were sorted into ten categories: Asellidae (isopods), Amphipoda (likely Gammaridae), Chironomidae (larvae and pupae), Cladocera, Copepoda, fish, Gastropoda, Ostracoda, Trichoptera, and other invertebrates (crayfish, bryozoan resting cells, bivalves, damselfly nymphs, ephippia, and Hydrachnidia). Prey items labeled “other invertebrates” were relatively rare and appeared in less than 5% of fish collected. The first 20 whole individuals of each prey taxa were measured and any additional individuals were only enumerated. The longest axis of whole invertebrates was measured to the nearest 10 µm and the total length of whole fish was measured to the nearest 1 mm. When only parts of an organism were present, only heads were counted, and length was estimated based on the average length of whole specimens measured in the same sample.

Fish carcasses (not including stomachs or otoliths) were ground for total lipid content analysis, following a modified version of the Folch et al. (1957) method, to test for seasonal differences in body lipid content. Total lipid content was reported as the percent of dry mass and was standardized by body mass (g). Most fish carcasses (n=600/791 samples; 76%) were analyzed for percent total lipid content. Samples from 2018 were not analyzed for percent total lipid content. Also, small, young-of-year fish were not included in lipid analyses because the dried samples lacked sufficient mass for replicate analyses. Briefly, each thawed fish was homogenized in a NutriBullet Original Blender (600 watts).
and a 50-g subsample (or the whole fish if fish < 50 g) was taken from the homogenate. Samples were dried to a constant mass at 65°C for 72 hours in an Isotemp oven (Fisher Scientific, Hampton, NH, USA). Once dry, samples were ground to a powder with a mortar and pestle. Three 1-g subsamples of homogenate from each fish were placed into pre-weighed 50-ml conical centrifuge tubes. We added 20 ml of a 2:1 chloroform:methanol solution to each centrifuge tube. Samples were mixed for 30 seconds using a vortex and centrifuged for 10 minutes at 2,056 RCF [GP Centrifuge GH-3.7 rotor, Beckman Coulter, Brea, CA, USA]. The lipid-containing supernatant was pipetted off and the process was repeated a second time. The resultant lipid-free pellets were then dried for 24 hours at 65°C to ensure any remaining chloroform:methanol solution had evaporated. Samples were weighed again in the centrifuge tubes and tube mass was subtracted from total mass to estimate the final lipid-free dry mass. Percent lipid content was calculated as the percent loss by mass of each subsample after lipid extraction. The values obtained from the three, 1-g subsamples were averaged to estimate percent total lipid content for each individual fish. Samples with coefficients of variation higher than 60% were not included in data analyses (Yellow perch = 336/346 samples, pumpkinseed = 67/71 samples, bluegill = 174/176 samples).

Seasonal variations in condition were estimated using Fulton’s condition factor (K):

\[
K = \left( \frac{W}{L^3} \right) \times 100
\]

where W is the wet mass (g) and L the total length (mm). Seasonal variation in condition within a population represents seasonal changes in the relative robustness or degree of
nourishment. Condition values, however, can also vary with fish age or sex. Population-level seasonal variations in condition and percent total lipid content were used to assess when energy was consumed and expended.

*Diet metrics*

Data from biweekly and monthly samples were pooled into seasons defined by water temperature and ice cover: autumn 2018 (09/27/2018 – 12/31/2018), winter (01/01/2019 – 04/14/2019), spring (04/15/2019 – 06/15/2019), summer (06/16/2019 – 09/13/2019), and autumn 2019 (09/14/2019 – 10/15/2019). Only fish with identifiable prey items in their stomachs were used in stomach content analyses (i.e., fish with empty stomachs or those with unidentifiable prey taxa were excluded). Wet mass (mg) was estimated for each individual prey item using length to dry mass and dry mass to wet mass conversion equations derived from literature sources (Table A.1). The masses of individual prey items were summed to obtain biomass totals for each prey taxon consumed by each fish. Percent diet compositions by count and biomass for each fish were pooled by season and averaged to obtain seasonal diet composition estimates. Diets were assessed by calculating the percentage of fish with empty stomachs, percentage of occurrence of each prey type in stomachs, and prey-specific abundance. Variations in the average number of diet items and average biomass within a predator species were used to evaluate seasonal differences in prey consumption. Amundsen et al. (1996) plots, made using biomass data, identified seasonal differences in diet composition, niche width, and feeding strategy in yellow perch and sunfishes.
Stomach content prey diversity was calculated using the Shannon diversity index (H; Shannon and Weaver 1998):

\[ H = - \sum_{i=1}^{s} p_i \ln p_i \]

where \( p_i \) is the proportion of each prey item \( i \) in the diet and \( s \) is the total number of unique prey taxa in the diet. Each individual fish, excluding those with empty stomachs, was assigned a prey diversity score, and variation in the average diversity score was used to assess seasonal changes in diet diversity.

Nonmetric multidimensional scaling (NMDS) ordination plots were constructed using Bray-Curtis distances to qualitatively identify and analyze seasonal variation in predator diet composition. NMDS plots were constructed for both numerical and biomass percent diet compositions using data pooled by sampling date. The NMDS analyses were conducted using the program R (version 3.5.2; R-Core Team) using the metaMDS() function in the vegan package (Oksanen et al. 2019).

Data analysis

Intra-species seasonal differences in the number of prey consumed were analyzed using three tests: ANOVA, Welch’s ANOVA, and the Kruskal-Wallis Rank Sum Test depending on data distributions. Subsequent post-hoc tests were conducted to determine pairwise differences in prey consumption between seasons. Yellow perch prey count data were normally distributed after a natural log transformation and a Welch’s ANOVA was
used on the transformed data because of heterogeneity of variances among the seasons. Pairwise t-tests with a Bonferroni correction were used to compare between groups. Pumpkinseed prey count data were normally distributed and had equal variances, among seasons, after a natural log transformation and a one-way ANOVA was used. Tukey’s HSD was used to compare between seasons. Bluegill prey count data had equal variances among groups but were not normally distributed; therefore, a Kruskal-Wallis Rank Sum Test was used. Pairwise Wilcoxon Rank Sum Tests with a Bonferroni correction were used to compare between seasons. Intra-species seasonal differences in the amount of prey consumed based on biomass were analyzed using the Kruskal-Wallis Rank Sum Test. Yellow perch and bluegill biomass data were inversely transformed. Pumpkinseed biomass data had equal variances, among seasons, without transformation. Pairwise Wilcoxon Rank Sum Tests with a Bonferroni correction were used to compare between seasons.

An analysis of similarity (ANOSIM) was used to quantitatively compare diet compositions among sampling dates and seasons. The test statistic R is constrained between the values -1 to 1, where positive numbers suggest more within-season similarity than between-season similarity among sampling dates, and values close to zero represent nearly random grouping. Therefore, R values closer to 1 would suggest seasonal differences in diet composition while R values close to zero would suggest that diets are similar among seasons. The statistical significance of R is assessed by permuting the grouping vector to obtain the empirical distribution of R under the null-model, in which the similarity between groups is greater than or equal to the similarity within the groups.
The ANOSIM function assesses differences among seasons but does not provide pairwise comparisons between seasons.

Schoener’s index of percentage overlap ($P_{jk}$) (Schoener 1970) was used to assess the similarity of diets between seasons. Intraspecies seasonal averages of prey counts and prey biomasses were used to calculate the percent overlap index. Normally, Schoener’s index is used to compare niche overlap between two potentially competing species; however, we used Schoener’s index to obtain a pairwise comparison matrix that describes in which seasons the diet compositions of a given species were similar. In addition, we used Schoener’s index to compare whether diet compositions of pumpkinseed and bluegill were similar within each season. Schoener’s index is calculated as:

$$P_{jk} = \left[ \sum_{i=1}^{n} \left( \min \{ p_{ij}, p_{ik} \} \right) \right]$$

where $p_{ij}$ is the proportion that resource $i$ is of the total resources used in season $j$, $p_{ik}$ is the proportion that resource $i$ is of the total resources used in season $k$, and $n$ is the total number of prey categories. Overlap values greater than 0.60 are considered to be biologically significant (Wallace 1981). The dietOverlap() function in the FSAmisc package was used to calculate Schoener’s index in R (Ogle 2015).

**Bioenergetics Modeling**

The Wisconsin bioenergetics model was used to estimate daily energy consumption ($C$) of yellow perch, pumpkinseed, and bluegill (Kitchell et al. 1977). Bioenergetics model
simulations were performed using Fish Bioenergetics 4.0 (FB4) (Deslauriers et al. 2017). The model was fit to observed annual growth of age-3 yellow perch, pumpkinseed, and bluegill in Keeler Bay. Sample sizes of other ages were too few to model. A bioenergetics model represents the energy budget of an individual:

\[
C = (R + A + SDA) + (F + U) + G
\]

where \(C\) = consumption, \(R\) = standard metabolism, \(A\) = energy expenditure due to activity, \(SDA\) = specific dynamic action (energy required to digest food), \(F\) = egestion, \(U\) = excretion, and \(G\) = growth. Standard metabolism is modeled as an exponential function of water temperature (Madenjian et al. 2017). Consumed energy is first allocated to metabolism \((R + A + SDA)\), some is lost as waste \((F + U)\) and the remainder is allocated to growth \((G)\). All calculations in the model are based on specific rates (i.e., joules per gram of predator per day). Growth can further be broken down into the three subunits somatic growth \((G_{somatic})\), gonadal growth \((G_{gonadal})\), or stored for future use \((G_{storage})\):

\[
G = G_{somatic} + G_{gonadal} + G_{storage}
\]

We modeled bioenergetics of yellow perch and bluegill separately using species-specific parameters (Kitchell et al. 1974, 1977) provided in the FB4 software (Deslauriers et al. 2017). Currently, no model parameters are available for pumpkinseed in FB4. Therefore, the bluegill model parameters were used for pumpkinseed input data. Model simulations ran on a daily timestep (Hewett and Johnson 1992) and began on September 27, 2018 (for pumpkinseed and bluegill) and October 23, 2018 (for yellow perch) and ended on October 15, 2019, for all three simulations.
Growth inputs (Table A.2) were mean mass at age-3 in October 2018 and the mean mass at age-4 in October 2019 for yellow perch. Pumpkinseed and bluegill mass-at-age data were pooled because of a lack of adequate sample sizes. The initial mass was the mean mass at age-3 in September 2018 and the final mass was the mean mass at age-4 in September 2019.

Diet Proportions

Fish diets were input into the FB4 model as the observed proportion of each prey taxon by wet biomass per day (see Diet metrics section). For each predator species, diet proportions of each individual, excluding fish with an empty stomach, were averaged by sampling date. Diet proportions were maintained for each model-day until the next sampling date when new diet data were available (Deslauriers et al. 2017; Madenjian et al. 2017; Pothoven et al. 2017).

Predator and Prey Energy Densities

Prey energy density values were based on previous studies (Table A.3). Seasonal variations in energy densities of common prey taxa have not been published; therefore, we retained constant values across seasons. The relationship between energy density and the dry-to-wet mass ratio of fishes has been well documented (Hartman and Brandt 1995; Ciancio et al. 2007; Johnson et al. 2017); therefore, we obtained wet and dry masses of individual fish and estimated energy density as a function of percent dry mass (Table A.4). We used a yellow-perch-specific model:
\[ ED = -2873 + 313.1 \, DM \]

where ED = energy density in J/g wet mass and DM = percent dry mass (Hartman and Brandt 1995). We also used a Perciform-family model for bluegill and pumpkinseed:

\[ ED = -1875 + 309.5 \, DM \]

where ED = energy density in J/g wet mass and DM = percent dry mass (Hartman and Brandt 1995). Using the approach presented here, energy density was allowed to change seasonally (Breck 2008).

Temperature

Daily lake temperature data were obtained from the Vermont EPSCoR Data Buoy located in Inner St. Albans Bay, Lake Champlain at an average depth of 3.5 m from September 01 to October 30 in 2018 and June 03 to November 11 in 2019 (Table A.5; Zia et al. 2016). Temperature data were collected every hour and were averaged to estimate mean daily temperature. Direct surface temperature measurements, taken using a handheld thermometer in Keeler Bay, were used when Vermont EPSCoR data were not available. Surface temperature measurements from Keeler Bay were not significantly different than temperature measurements from Inner St. Albans Bay (Paired t-test, \( t_8 = 2.31, p = 0.651 \)).

Fish body temperatures are equal to or within a few fractions of a degree of the surrounding water temperature (Wood and McDonald 1997; Beitinger et al. 2000); therefore, we modeled the temperature experienced by a fish similar to Kao et al. (2015). We assumed that fish behaviorally thermoregulate by occupying habitats in which
temperatures are within their preferred temperature range when available. We used the mean optimum growth temperature (OGT) of 25°C for yellow perch and pumpkinseed and a mean OGT of 29°C for bluegill (Hasnain et al. 2010). When water temperatures were lower than the mean OGT, we used the warmest temperature available to approximate the temperature experienced by the modeled fish. In winter, we assumed that the modeled fish would stay at a depth where the temperature is the warmest relative to surface temperatures, modeled as 4.0°C.

Daily temperature was modeled as the minimum temperature value between the ambient water temperature near 3.5 m depth and the mean optimum growth temperature (Kao et al. 2015):

\[ T_{exp}(t) = \min [T_{OGT}, T_{amb}(t)] \]

where \( T_{exp}(t) \) is the temperature (°C) experienced by the modeled fish on day \( t \), \( T_{OGT} \) is the mean optimum growth temperature of the fish, and \( T_{amb}(t) \) is the ambient water temperature near 3.5 m depth on day \( t \). For example, when modeling yellow perch, ambient water temperatures were always used except when ambient water temperatures exceeded 25°C, in which case, the OGT of 25°C was used.

**Reproduction**

Gametes are produced using energy allocated to growth, and energy stored in gametes is lost when fish spawn. One of the main assumptions of the bioenergetics model is that the gonad energy density is equal to the whole-body energy density of the spawning fish;
such an assumption will underestimate the energetic loss in spawning females but overestimate in males (Deslauriers et al. 2017). Spawning day was assigned as April 01, 2019, for yellow perch, June 01, 2019, for pumpkinseed, and July 01, 2019, for bluegill. The maximum gonadosomatic index value measured for each species prior to spawning was used as the percentage of body mass lost on the spawning day. Spawning was simulated as a loss of body mass of 21% in yellow perch, 9% in pumpkinseed, and 11% in bluegill.

**Results**

We collected 400 yellow perch (n= 102 autumn, n= 122 winter, n= 99 spring, n=77 summer), 163 pumpkinseed (n= 71 autumn, n= 34 winter, n= 7 spring, n= 51 summer), and 228 bluegill (n= 48 autumn, n= 124 winter, n= 1 spring, n= 55 summer) from September 2018 until October 2019. The lake level of Lake Champlain rose and flooded the nearshore woodland zone during the spring of 2019 until mid-June (U.S. Geological Survey 2019), and few sunfish (n= 8) were caught during this time. Sunfish were not included in stomach content analyses due to low sample sizes.

Yellow perch, pumpkinseed, and bluegill foraged in every season sampled, although seasonal variation in foraging intensity occurred among individuals and among populations (Fig. 2.2, Table A.6). In yellow perch, the percentage of fish caught with empty stomachs was high in autumn 2018 (39%, total catch=44) and winter (34%, total catch=122), and lowest in spring (8%, total catch=99) and summer (10%, total catch=77). Similarly, in pumpkinseed, the percentage of fish caught with empty stomachs was
highest in winter (76%, total catch=34) but below 40% in all other seasons. Bluegill exhibited a similar trend as pumpkinseed. The percentage of bluegill caught with empty stomachs was highest in winter (51%, total catch=124), and lowest in autumn 2018 (6%, total catch=17) and summer (5%, total catch=55). Thus, all predator populations foraged more frequently in summer and decreased foraging in autumn and winter.

The average number of diet items per stomach and the average diet biomass consumed by an individual varied by season for each predator species (Table 2.1). In yellow perch, the average number of diet items was significantly different among seasons (Welch’s ANOVA, F4, 108.61 = 29.717, p < 0.001). Yellow perch stomachs contained the highest average number of diet items in summer (528.4 – zooplankton dominated, SE = 98.51) and lowest in winter (10.5, SE = 1.50). The average number of diet items in summer was significantly higher than all other seasons (Pairwise t-tests, p < 0.05) and the average number of diet items in winter was significantly lower than spring and summer values (p < 0.001) but not significantly different than autumn 2018 or autumn 2019 (p > 0.06). The average number of diet items in autumn 2018 was not significantly different from autumn 2019 (p = 0.87). The average diet biomass of yellow perch was significantly different among seasons (Kruskal-Wallis Rank Sum Test, H= 30.949, d.f. = 4, p < 0.001). Yellow perch stomachs contained the highest average diet biomass in autumn 2018 (1,472.8 mg, SE = 335.44) and lowest in autumn 2019 (91.3 mg, SE = 34.25). The average diet biomass in autumn 2019 was significantly lower than all other seasons (Pairwise Wilcoxon Rank Sum Tests, p < 0.02). The average diet biomass in autumn 2018 was significantly higher than all other seasons (p < 0.05) except summer (p = 0.08). The
average diet biomasses in winter, spring, and summer were not significantly different from one another (P > 0.50). Thus, yellow perch consumed the highest number of prey in summer, which reflected in large diet biomass. Note, on average, few prey were consumed in winter, yet the average diet biomass was large.

The average number of diet items, in pumpkinseed, was significantly different among seasons (ANOVA, F_{3,86}= 2.988, p = 0.036). Pumpkinseed stomachs contained the highest number of diet items in autumn 2018 (17.0, SE= 2.75) and the lowest in winter (4.1, SE= 1.04). The average diet count in winter was significantly lower than in autumn 2018 (Tukey’s HSD, p = 0.036) but not significantly different than any other season. The average diet biomass of pumpkinseed was also significantly different among seasons (Kruskal-Wallis Rank Sum Test, H = 10.404, d.f. = 3, p = 0.015). Pumpkinseed stomachs contained the highest average diet biomass was in winter (84.2 mg, SE= 27.32) and lowest in autumn 2019 (6.9 mg, SE= 2.26). The average diet biomass in winter was significantly higher than autumn 2018 (Pairwise Wilcoxon Rank Sum Tests, p = 0.055) and autumn 2019 (p = 0.027) but not significantly different than summer. Pumpkinseed consumed many prey items in summer and this foraging resulted in a large diet biomass. Interestingly, pumpkinseed consumed the fewest prey items, on average, in winter; however, winter prey items resulted in the largest average diet biomass among all other seasons.

In bluegill, the average number of diet items was significantly different among seasons (Kruskal-Wallis Rank Sum Test, H= 62.860, 3 d.f., P < 0.001). Bluegill stomachs contained the highest number of diet items in summer (152.2 - zooplankton dominated,
SE= 78.19) and the lowest in winter (9.0, SE=2.55). The average number of diet items was significantly lower in winter than all other seasons (Pairwise Wilcoxon Rank Sum Tests, P < 0.001). The average diet biomass of bluegill was significantly different among seasons (Kruskal-Wallis Rank Sum Test, $H = 12.786$, 3 d.f., $P = 0.005$). Bluegill stomachs contained the highest diet biomass in summer (80.7 mg, SE = 26.33) and the lowest in winter (24.1 mg, SE = 4.73). The average diet biomass in autumn 2018 was significantly different than autumn 2019 (Pairwise Wilcoxon Rank Sum Tests, $p < 0.001$) and winter ($p = 0.024$). Thus, bluegill consumed the most prey items in summer, with a large average diet biomass. Conversely, bluegill consumed the fewest prey items in winter, with a small average diet biomass. No bluegill were caught that contained diet items in the spring.

*Diet composition*

Diet composition changed seasonally in terms of count and biomass for each predator species (Fig. 2.3). The species richness and diversity of yellow perch prey was highest in spring (mean Shannon Diversity Score, $H = 0.72$, SE= 0.05) and lowest in autumn 2018 (mean $H= 0.11$, SE= 0.05) (Fig. 2.5, Table A.6). Yellow perch fed on a large variety of prey types in all seasons, including amphipods, chironomids, and fishes. Cladocerans were important in spring and summer but were infrequently eaten in autumn and winter. Isopods were one of the most important prey items for yellow perch in winter and, to a lesser degree, in spring. Fish were not frequently eaten but, because of their mass, contributed greatly to the diet of yellow perch in terms of biomass consumed.
The species richness and diversity of pumpkinseed prey were highest in autumn 2018 (mean Shannon Diversity Score (H)= 0.95, SE= 0.06) and lowest in winter (mean H= 0.17, SE= 0.11) (Fig. 2.5, Table A.6). Pumpkinseed fed on a large variety of prey types in all seasons, whereas fewer prey types, mainly amphipods, chironomids, and isopods, dominated their diets during winter. In summer and autumn, pumpkinseed had a more diverse diet that included copepods, cladocerans, trichopterans, and gastropods.

The species richness and diversity of bluegill prey was highest in autumn 2018 (mean Shannon Diversity Score (H)= 1.26, SE= 0.11) and lowest in winter (mean H= 0.29, SE= 0.05) (Fig. 2.5, Table A.6). Bluegill fed on a variety of prey types in all seasons except spring for which there are no data. Similar to pumpkinseed, bluegill diets were dominated by amphipods and chironomids in all seasons. Trichoptera were of particular importance to the bluegill diet in all seasons except winter. Cladocerans were consumed most frequently in summer. Numerically, bluegill had a diverse diet composition in summer and autumn; however, small prey types such as ostracods did not contribute greatly to the overall biomass consumed. Amphipods, chironomids, and isopods dominated the winter diet of bluegill, similar to pumpkinseed; however, bluegill also consumed cladocerans and copepods in winter.

Amundsen plots (Amundsen et al. 1996) identified seasonal differences in diet composition and feeding strategy in yellow perch and sunfishes (Fig. 2.4). The winter diet of yellow perch was dominated by isopods and amphipods, and to a lesser extent, prey fish. Conversely, the summer was dominated by cladoceran, autumn 2018 by prey fish, and autumn 2019 by chironomids. Spring diets were not dominated by a single prey
taxa but rather consisted of a diverse diet. Prey fish clustered in the upper left of the
Amundsen plot, which indicates that prey fish are consumed by a few individuals
displaying specialization. The majority of prey taxa were low in prey-specific abundance
which indicates that yellow perch have a generalist feeding strategy throughout all
seasons.

Isopods, and to a lesser extent, chironomids dominated the winter diet of pumpkinseed
(Fig. 2.4). Amphipods were dominant in summer and autumn 2018. Autumn 2019 diets
were not dominated by a single prey taxa but rather consisted of a diverse diet. Unlike
yellow perch, pumpkinseed shifted from a generalist feeding strategy in autumn to a
specialist feeding strategy in winter.

The dominant prey taxa of bluegill varied seasonally (Fig. 2.4). Isopods, and to a lesser
extent, amphipods and chironomids dominated the diet in winter. Cladocera and
Trichoptera were dominant in summer, and Amphipoda and Trichoptera in autumn.
Similar to pumpkinseed, bluegill displayed a generalist feeding strategy in the open-water
seasons but specialized on isopods in winter. Bluegill and pumpkinseed diets were
dominated by the same prey taxa in winter and autumn.

Nonmetric multidimensional scaling (NMDS) also identified seasonal differences in diet
composition in all three predator species. Ordination resulted in convergent solutions for
percent diet composition based on count and biomass values. In yellow perch, the winter
diet was diverse and there was variability in diet composition among sampling dates (Fig.
2.6). The diet composition by count (ANOSIM, R= 0.506, p = 0.001) and biomass (R =
0.339, \(p = 0.011\) of yellow perch were significantly different among seasons. Isopods and amphipods, which dominated the diet by count and biomass, drove the separation of winter from the other seasons. Spring and summer diet compositions were ordinated similarly around cladocerans, gastropods, ostracods, and Trichoptera.

The diet composition by count (ANOSIM, \(R= 0.20, p = 0.129\)) and biomass (\(R= 0.206, p = 0.149\)) of pumpkinseed were not significantly different among seasons (Fig. 2.7). In both the numerical NMDS and biomass NMDS, autumn 2018, autumn 2019, and summer 2019 were clustered together and ordinated around amphipods, cladocerans, copepods, gastropods, trichopterans. The winter diet composition of pumpkinseed was dominated by isopods, and to a lesser extent, chironomids which drove the separation from other seasons.

The diet composition by count (ANOSIM, \(R= 0.593, p = 0.002\)) and biomass (\(R= 0.638, p = 0.001\)) of bluegill were significantly different among seasons (Fig. 2.8). Isopods and chironomids dominated the winter diet by count, whereas isopods and amphipods dominated the winter diet by biomass. Autumn 2019, summer, and autumn 2019 diet compositions were dominated by chironomids, gastropods, ostracods, and trichopterans. While the ANOSIM results report differences in diet composition among seasons, pairwise comparisons are unavailable in the ANOSIM function.

*Seasonal diet overlap*

Intra-species seasonal differences in diet composition by count and biomass were determined using Schoener’s percent overlap index. In yellow perch, the diet composition
by prey count in spring 2019 significantly overlapped the diet composition in summer 2019 ($P_{jk} = 0.74$), while all other comparisons did not significantly overlap ($P_{jk} < 0.60$, Table 2.2). In terms of diet composition by biomass, the winter and spring 2019 diets significantly overlapped ($P_{jk} = 0.76$), as did autumn 2018 and 2019 ($P_{jk} = 0.68$, Table 2.2). In pumpkinseed, the diet composition by prey count in autumn 2018 significantly overlapped the diet composition in summer 2019 ($P_{jk} = 0.74$) and autumn 2019 ($P_{jk} = 0.64$, Table 2.3). In addition, the summer and autumn 2019 diets significantly overlapped ($P_{jk} = 0.70$). In terms of diet composition by biomass, the autumn 2018 and summer 2019 diets significantly overlapped ($P_{jk} = 0.84$, Table 2.3). In bluegill, no pairwise diet overlap comparisons were significant (Table 2.4).

The seasonal comparison of diet composition by count and biomass between pumpkinseed and bluegill indicated significant overlap in almost every season (Table 2.5). In terms of diet composition by count, pumpkinseed and bluegill diets significantly overlapped in autumn 2018 ($P_{jk} = 0.80$) and 2019 ($P_{jk} = 0.63$). In terms of diet composition by biomass, pumpkinseed and bluegill diets significantly overlapped in autumn 2018 ($P_{jk} = 0.82$), winter 2019 ($P_{jk} = 0.66$), and autumn 2019 ($P_{jk} = 0.68$). Unfortunately, insufficient sample sizes did not allow for a comparison of spring 2019 diets. These analyses suggest that the two species of genus *Lepomis* consume similar prey items in three of five seasons studied.
Percent total lipid content, condition, and gonadosomatic index

Percent total lipid content and body condition fluctuated seasonally in all three predator species. In yellow perch, percent total lipid content was highest in July and lowest in March (Fig. 2.9), and highly variable in May, likely around the same time that yellow perch were spawning (Fig. 2.10). Lipids accumulated from May until July and decreased throughout the late summer and autumn. Late autumn values were similar to values obtained in winter. Seasonal trends in percent total lipid content did not vary between sexes. In pumpkinseed, there was seasonal variation in percent total lipid content (Fig. 2.9). Values were lowest in winter and increased in the summer. The seasonal variation in lipid content in pumpkinseed was roughly similar to the seasonal trend found in yellow perch but lipid content was highest in late summer and autumn. In bluegill, there was sex-based and seasonal variation in percent total lipid content (Fig. 2.9). Lipid content was lowest in March and increased through the summer and autumn. The seasonal variation in lipid content in bluegill was not similar to pumpkinseed.

Body condition followed similar seasonal trends as percent total lipid content in each predator species (Fig. 2.11). In yellow perch, females often had higher condition than males; however, both sexes followed a similar seasonal pattern. Condition increased through the winter until a decrease in April and May. In pumpkinseed, condition appeared to increase over the winter and summer and decrease in autumn. In bluegill, condition was stable throughout the winter but increased in summer.
The gonadosomatic index varied seasonally for all three predator species and showed differences in the timing of gametogenesis (Fig. 2.10). Yellow perch began gonad development in early autumn and continued through the winter before spawning in May. Conversely, bluegill did not begin gonad development until after ice-out in April 2019 and spawned sometime after July. There were no trends in the gonadosomatic index data of pumpkinseed.

*Bioenergetics model simulations*

Consumption rates and metabolic rates varied seasonally for each species (Fig. 2.12, Fig. 2.13). Yellow perch daily consumption rates were 6.0 times higher and metabolic rates were 5.3 times higher in summer than in winter. Consumption rates exceeded metabolic rates for the entire modeled period but the ratio of metabolic costs to energy consumption (M/C) varied seasonally (Fig. 2.13). M/C had a bimodal distribution with the highest values in February and July. High M/C in February resulted from low consumption rates in winter while high M/C in July resulted from high metabolic rates in summer. The lowest M/C occurred in months with moderate consumption and cool water temperatures. Modeled growth rates were lowest in July which indicates that metabolic costs exceeded energy consumption (Fig. 2.12). In winter, growth rates were lowest in February but were otherwise positive.

Pumpkinseed daily consumption rates were 10.6 times higher and metabolic rates were 5.7 times higher in August than in February (Fig. 2.12). Consumption rates exceeded metabolic rates in all months except February, but M/C varied seasonally (Fig. 2.13).
Unlike yellow perch, pumpkinseed M/C had a unimodal distribution; pumpkinseed M/C increased throughout autumn, had the highest values in throughout the winter, and gradually decreased in spring. The lowest M/C occurred in months with high consumption and warm water temperatures. Unlike yellow perch, pumpkinseed growth rates were negative throughout the winter. In combination, these results indicate that metabolic costs greatly exceeded energy consumption throughout the winter and energy reserves were depleted to meet metabolic demands (Fig. 2.12).

Bluegill consumption rates were 17.8 times higher and metabolic rates 6.2 times higher in July than in February (Fig. 2.12). Consumption rates exceeded metabolic rates in all months except January through March, and M/C varied seasonally (Fig. 2.13). Similar to pumpkinseed, bluegill M/C had a unimodal distribution; bluegill M/C increased throughout autumn, had the highest values in throughout the winter, and gradually decreased in spring. The lowest M/C proportions occurred in months with high consumption and warm water temperatures. Similar to pumpkinseed, bluegill growth rates were negative throughout the winter and early spring. These results indicate that metabolic costs greatly exceeded energy consumption throughout the winter and energy reserves were depleted to meet metabolic demands (Fig. 2.12).

**Discussion**

Here, we empirically show that winter foraging behavior and seasonal energy dynamics likely depend on the thermal preference of individual fish species. Our results support our first hypothesis that cool-water species forage in all seasons, including winter, whereas
warm-water species forage in the open-water seasons but exhibit reduced foraging in the winter. Our results also support our second hypothesis that winter foraging provides sufficient energy for overwinter growth in cool-water species but does not in warm-water species.

Each fish species consumed a large variety of prey types, but the species richness and diversity of the diets declined in winter, especially in sunfish, and were often dominated by isopods, amphipods, and chironomids. Yellow perch consumed more prey in winter, in terms of count and biomass, than either of the sunfishes. Yellow perch exhibited a generalist feeding strategy in winter while sunfishes, when they did eat, specialized on only a few taxa. Conversely, the prey diversity of yellow perch in Lake Mendota, Wisconsin decreases from summer to winter (Pearse and Achtenberg 1920; Hasler 1945). Yellow perch consume primarily benthic prey in winter, whereas summer diets were more diverse and included pelagic prey. Freshwater isopods inhabit areas of aquatic vegetation (Wilson 2008), which explains why they are commonly found in our diet results. Overwintering zooplankton were consumed by yellow perch and bluegill in our study. Although densities of most zooplankton are often at annual lows during winter, some species overwinter and have high lipid concentrations which may allow for the transfer of high-quality energy to higher trophic levels (Syväranta & Rautio 2010; Grosbois et al. 2017; Hampton et al. 2017; Schneider et al. 2017; Mariash et al. 2017).

Fish are likely to shift their diets as different prey resources and trophic levels become available throughout the year. Seasonal shifts in prey diversity, from surface invertebrates to benthic invertebrates, have been reported in cold-water species such as Arctic charr.
and brown trout *Salmo trutta* (Amundsen and Knudsen 2009). Similarly, zooplankton can subsidize the predominantly benthivorous diet of Arctic charr in subarctic lakes (Eloranta et al. 2013). When cisco spawn in Lake Superior, lake whitefish shift their diets from benthic invertebrates to the highly abundant and energetic cisco eggs (Stockwell et al. 2014). Thus, the ability of predators to be generalists and consume whatever prey are available likely ensures continued survival in temporally variable food webs (McMeans et al. 2015).

Whether winter prey taxa are targeted due to their relatively high abundances in winter, their ease of capture, or their high lipid content, as suggested by optimal foraging theory (Werner and Hall 1974), remains untested and may be a fruitful avenue of future research. Isopods are likely easy to capture and may explain why they are dominant within the sunfish winter diets. Conversely, yellow perch consumed zooplankton and prey fish in winter and did not appear to preferentially select slow-moving prey solely to conserve energy in winter. Therefore, the winter diet preferences of cool-water fish may be related to prey availability, whereas the winter diet preferences of warm-water fish may be related to the ease of capture and conservation of energy.

Our results show that winter foraging provides sufficient energy for overwinter growth in yellow perch but not in the sunfishes. Modeled growth rates for yellow perch were predicted to be lowest in winter but were above zero. Bioenergetics results suggest that yellow perch obtain surplus energy throughout the winter. Lipids, which are catabolized to meet energetic demands, were also at annual lows in winter but did not reach critical levels associated with starvation (Finstad et al. 2010). Lipid reserves are likely to vary
based on the latitudinal position of a fish population but may be exceeded by energetic demands at extremely high latitudes, which may explain the northern distributional limits of some temperate fishes (Shuter and Post 1990; Berg et al. 2009). Therefore, yellow perch populations at higher latitudes, with longer winters, may require more energy to meet metabolic demands in winter than populations in Lake Champlain and may not exhibit similar bioenergetic results.

Yellow perch in temperate lakes likely use assimilated energy for gametogenesis over the winter (Dabrowski et al. 1996). At colder temperatures, yellow perch produce eggs of higher quality, containing more unsaturated fatty acids (Feiner et al. 2016). Yellow perch produce lower quality eggs of smaller size following warm winters in Lake Erie, which are becoming more frequent due to climate change (Farmer et al. 2014). Female walleye *Sander vitreus* in Lake Erie require sufficient surplus energy to provide an energy reserve before, during, and after spawning (Henderson and Nepszy 1994). Thus, the energy gained and depleted during winter may not only affect individual survival but also future reproductive output and population dynamics (Reznick and Braun 1987; Hurst 2007; Brodersen et al. 2011).

Unlike yellow perch, the sunfishes ate infrequently in winter, and of those that did eat, winter diets were small in terms of count and biomass. We observed continued depletion of stored energy from the onset of winter until spring. Percent total lipid content and body condition of both sunfish species were lowest in winter. Bioenergetics simulations suggest that energetic costs exceeded consumed energy in most winter months. Our results indicate that sunfish likely remain inactive during winter, minimize energetic
demands, and feed opportunistically. Intervals of opportunistic feeding, when prey are nearby or easily ingested, may reduce the rate at which stored energy is depleted in winter by occasionally supplementing energy reserves (Johnson and Evans 1991; Shuter et al. 2012; Speers-Roesch et al. 2018). Unlike yellow perch which spawn soon after ice-out, sunfish in Vermont do not spawn until June and July and forgo gonad development until ice-out. Warm-water fish have time between the end of winter and spawning to forage and consume sufficient energy to grow gametes as suggested by the energy consumption rates in our bioenergetics models. Thus, warm-water fishes, e.g., pumpkinseed and bluegill, are likely to merely endure winter and minimize energetic expenditures through prolonged inactivity.

The seasonal energy dynamics of cold-water, autumn-spawning fish are distinct from the seasonal energy dynamics of spring-spawning fish and can be juxtaposed to highlight differences in terms of winter foraging (Suski and Ridgeway 2009; Shuter et al. 2012; Fernandes and McMeans 2019). Unlike spring-spawning fish, cold-water fish spawn in late autumn so winter is a post-spawning period and foraging may be used to restore lost energy reserves. Adult Arctic charr and brown trout actively fed in winter in Lake Fjellfrøsvatn, Norway; however, individuals did not exhibit growth and condition decreased (Amundsen and Knudsen 2009). Alternatively, juvenile lake trout in Lake Champlain grew in length over the winter while body condition was maintained, which suggests energy was consumed and assimilated in winter (Wilkins 2019). Of special note is the freshwater burbot *Lota lota* which is an unusual species unlike any other cold-water fish residing in temperate lakes. Burbot are true winter specialists and exhibit extremely
low temperature preferences, which allows them to forage, grow, and reproduce during the winter months and causes them to be least active during the summer months (Hölker et al. 2004; Harrison et al. 2016; Grabowski et al. 2020). The enzymatic specializations that allow cold-water fish to optimally function in cold waters also likely allow them to gain an energetic benefit from winter foraging (Shuter et al. 2012). Thus, the energetic consequences of winter activity differ among thermal guilds.

Due to the nature of winter fish work, there were limitations in our modeling and data collection methods. First, prey energy density values used in our models were borrowed from literature sources and do not vary seasonally, an issue that has been raised by numerous authors as a source of error in bioenergetics modeling (Kao et al. 2015; Deslauriers et al. 2017; Madenjian et al. 2017; Pothoven et al. 2017). Seasonally variable site-specific values for prey energy densities are ideal, although costly to obtain, and future research on this topic would be extremely beneficial. Second, angling is a biased sampling method that may inadvertently target particular size or age classes, and angled fish may be more likely to be actively feeding individuals. However, angling yielded the highest catch rates. We attempted short-term (3-hr) under-ice gillnet sets, as described in Block et al. (2019), but did not catch any fish. Third, we captured relatively few large individuals of any fish species, hence our conclusions are largely based on small fish. The size range of fish collected in this study is similar to the size range of fish found in other populations throughout Lake Champlain (Pientka 2017). Also, there was no indication of any differences in foraging intensity based on age. Keeler Bay is a nursery habitat for cool- and warm-water fishes, and larger individuals likely move out of the bay and into
the open lake. Therefore, our results are representative of Keeler Bay and not Lake Champlain as a whole. Likely, our results would vary based on lake morphology, ice cover duration, and local temperature regimes. Populations of each species may differ in diet and seasonal energy dynamics depending on local conditions.

Winter lake conditions will change due to global climate warming. Mean winter water temperatures have increased globally and will likely continue to increase based on future climate change projections (Gerten and Adrian 2000; George et al. 2007; Hewitt et al. 2018). Seasonal ice cover duration will continue to decrease in the coming decades; consequently, lakes will be ice-free more often in winter than in the past and light penetration will be greater during ice-free winters (Magnuson et al. 2000; Weyhenmeyer et al. 2011; Hampton et al. 2017). Thus, climate change is expected to affect fish directly due to temperature and light effects on consumption and metabolism (Walther et al. 2002; Hurst 2007; Brodersen et al. 2011). Warmer water temperatures will increase metabolic rates in fish; however, whether projected increases in water temperatures would decouple the existing bioenergetic relationships is unclear (Clarke and Johnston 1999). If metabolism increases at a rate that is not matched by increased energy consumption, then less assimilated energy is available for growth. Fish species with dissimilar temperature optima and diverse adaptations to low temperatures will respond differently to climate-driven increases in winter water temperatures (Hasnain et al. 2010; Shuter et al. 2012; Kao et al. 2015). Cool-water fish such as yellow perch would likely benefit from increased water temperatures as long as consumed energy exceeds metabolic costs. Conversely, warm-water species such as sunfishes, carp *Cyprinus carpio*, or muskellunge
*Esox masquinongy* may suffer from increased winter water temperatures because faster metabolic rates would more rapidly draw down energy stores. Alternatively, warm-water fishes may be able to forage more effectively at slightly warmer water temperatures, but a critical prey density still needs to be available in winter for energy consumption to exceed increased metabolic demands (Garvey et al. 2004; Byström et al. 2006; Finstad et al. 2010). Cold-water adapted species such as Arctic charr, brown trout, or lake trout may be even more vulnerable to increased water temperatures because of the potential of competition with invading warm-water species, and reductions in hypolimnetic habitat size and increased hypolimnetic oxygen deficits in summer (Shuter et al. 2012). Therefore, increased water temperatures have the potential to benefit or harm fish growth, depending on an available food supply (Garvey et al. 2004; Byström et al. 2006; Brodersen et al. 2011).

Higher light levels, due to ice-free winters, may positively or negatively affect winter foraging and the seasonal energy dynamics of fish. Fish that rely on visual predation would be able to forage more efficiently or for a longer period than when lakes are ice-covered (Jacobsen et al. 2002). In lakes with high primary productivity, winter light levels can exceed summer light levels; therefore, fish may have the potential for better visual foraging success in winter than in summer (e.g., Hergenrader and Hasler 1968). More light may also increase foraging success for fishes that inhabit brownified, humic lakes (Hedström et al. 2017). Increased foraging success would increase energy consumption and growth. However, more light may cause an increase in fish metabolic rates. A combination of darkness and cold water temperatures significantly decreases the
activity and metabolic rates of the winter-inactive wrasse, cunner *Tautogolabrus adspersus* (Speers-Roesch et al. 2018). In response to increased light levels, cunner increased their activity and metabolic rates. Therefore, a significant increase in light penetration, caused by decreased ice cover, would likely increase activity and subsequently metabolic rates in fish. Winter-inactive species would be negatively affected by faster metabolic rates because energy reserves would be depleted at a faster rate than under low-light conditions. If metabolism increases at a rate not matched by increased foraging ability and energy consumption, then less assimilated energy is available for growth. Changes in both ambient light levels and water temperatures in winter have the potential to affect the seasonal energy dynamics of individuals and populations.

In summary, our data show that cool-water fish (yellow perch) forage and gain sufficient energy for growth in all seasons, including winter, whereas warm-water fish (pumpkinseed and bluegill forage in the open-water seasons and have reduced foraging and no growth in the winter. Winter foraging does occur in the cool-water and warm-water thermal guilds and the consequences of winter foraging are different among these guilds. However, our study was limited to only one cool-water species and two warm-water species, and our results may not apply to all other members of these thermal guilds. Cool-water species that spawn in spring likely use energy gained in the winter to develop gonads, while warm-water species merely survive the winter and use previously stored energy to endure. The relationships between winter foraging and seasonal energy dynamics of these fishes will likely be altered due to climate change. Decreased ice cover
duration and increases in water temperatures and ambient light will likely disrupt the mechanisms that these species have evolved to tolerate winter conditions in temperate lakes. Thus, changes to the seasonal energy dynamics of fishes would not only affect individual survival but also reproductive success and the transfer of energy through food webs.
Acknowledgments

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Tables and Figures

Table 2.1: The mean number and mean biomass of prey items by season for three predator species collected in Keeler Bay, Lake Champlain in 2018-2019. BG – bluegill, PS – pumpkinseed, YP – yellow perch. N is the number of fish of a given species caught in each season and SE is the standard error.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>N</th>
<th>Mean # of prey items</th>
<th>SE</th>
<th>Mean biomass of prey items</th>
<th>SE</th>
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<tbody>
<tr>
<td>BG</td>
<td>Autumn 2018</td>
<td>16</td>
<td>54.1</td>
<td>11.78</td>
<td>42.5</td>
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<td>BG</td>
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<td>27</td>
<td>29.1</td>
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<td>10.5</td>
<td>1.50</td>
<td>171.3</td>
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Table 2.2: Schoener’s diet overlap index matrix for yellow perch based on prey counts and biomass. Yellow perch were collected in Keeler Bay, Lake Champlain in 2018-2019. Values represent inter-seasonal overlap in diet similarity. Values greater than 0.60 represent high overlap (similarity).

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<td>Diet overlap based on biomass</td>
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Table 2.3: Schoener’s diet overlap index matrix for pumpkinseed based on prey counts and biomass. Pumpkinseed were collected in Keeler Bay, Lake Champlain in 2018-2019. Values represent inter-seasonal overlap in diet similarity. Values greater than 0.60 represent high overlap (similarity).

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<tr>
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<td><strong>Diet overlap based on biomass</strong></td>
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<tr>
<td>Autumn 2018</td>
<td>-</td>
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Table 2.4: Schoener’s diet overlap index matrix for bluegill based on prey counts and biomass. Bluegill were collected in Keeler Bay, Lake Champlain in 2018-2019. Values represent inter-seasonal overlap in diet similarity. Values greater than 0.60 represent high overlap (similarity).

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<td>Diet overlap based on count</td>
<td>Diet overlap based on biomass</td>
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<tr>
<td>Autumn 2018</td>
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Table 2.5: Schoener’s diet overlap index matrix to compare the seasonal similarity of diets between pumpkinseed and bluegill based on prey counts and biomass. Pumpkinseed and bluegill were collected in Keeler Bay, Lake Champlain in 2018-2019. Values represent inter-seasonal overlap in diet similarity. Values greater than 0.60 represent high overlap (similarity).

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<tr>
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<td>-</td>
<td>0.30</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.63</td>
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| Diet overlap based on biomass |              |             |             |             |             |
| Autumn 2018       | 0.82        | -           | -           | -           | -           |
| Winter 2019       | -           | 0.66        | -           | -           | -           |
| Spring 2019       | -           | -           | -           | -           | -           |
| Summer 2019       | -           | -           | -           | 0.43        | -           |
| Autumn 2019       | -           | -           | -           | -           | 0.68        |
Fig. 2.1: Study area of Keeler Bay, Lake Champlain. Contours are at 2-m intervals. The inset map is of Lake Champlain from Crown Point northward. The location of Keeler Bay in Lake Champlain is highlighted by the black, square box in the inset map. VT = Vermont, NY = New York, and QC = Quebec.
Fig. 2.2: Percent of fish caught with empty stomachs by season in three species collected in Keeler Bay, Lake Champlain in 2018-2019. Values above bars are the number of fish of a given species caught in each season.
Fig. 2.3: Percent diet composition by prey count and biomass for three species collected in Keeler Bay, Lake Champlain in 2018-2019.
Fig. 2.4: Amundsen plots that represent seasonal differences in diet composition based on biomass, niche width, and feeding strategy in yellow perch (A), pumpkinseed (B), and bluegill (C) collected in Keeler Bay, Lake Champlain in 2018-2019. Prey-specific abundance is defined as the percentage of prey taxon biomass which composes total biomass in only those predators in which the actual prey occurs. The frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs. Information about prey importance and feeding strategy of the three predator species can be obtained by examining the distributions of points along the diagonals and axes of the Amundsen plots (Amundsen et al. 1996).
Fig. 2.5: Seasonal variation in Shannon’s diversity index (H) for three species collected in Keeler Bay, Lake Champlain in 2018-2019. Dots represent outliers that are 1.5*interquartile range.
Fig. 2.6: Nonmetric multidimensional scaling analyses of yellow perch diet composition by (A) numerical prey composition (stress= 0.14) and (B) biomass prey composition (stress= 0.15). Two axes were selected for ordination. Taxa closer to a sampling date (point) make up a larger portion of the diet than those farther apart. Point shape and polygon color represent which season the sampling date is from.
Fig. 2.7: Nonmetric multidimensional scaling analyses of pumpkinseed diet composition by (A) numerical prey composition (stress= 0.05) and (B) biomass prey composition (stress< 0.001). Two axes were selected for ordination. Taxa closer to a sampling date (point) make up a larger portion of the diet than those farther apart. Point shape and polygon color represent which season the sampling date is from.
Fig. 2.8: Nonmetric multidimensional scaling analyses of bluegill diet composition by (A) numerical prey composition (stress= 0.04) and (B) biomass prey composition (stress= 0.05). Two axes were selected for ordination. Taxa closer to a sampling date (point) make up a larger portion of the diet than those farther apart. Point shape and polygon color represent which season the sampling date is from.
Fig. 2.9: Percent total lipid content (% of dry mass) per gram of body mass by month. Yellow perch (A), pumpkinseed (B), and bluegill (C) were collected in Keeler Bay, Lake Champlain in 2019. Dots represent outliers that are 1.5*interquartile range. Note, horizontal lines that are not within a boxplot are single fish rather than mean values.
Fig. 2.10: Gonadosomatic index (GSI) by month of male and female yellow perch (A), pumpkinseed (B), and bluegill (C) collected in Keeler Bay, Lake Champlain in 2019. Dots represent outliers that are 1.5*interquartile range. Note, horizontal lines that are not within a boxplot are single fish rather than mean values.
Fig. 2.11: Body condition (Fulton’s K) by month of yellow perch (A), pumpkinseed (B), and bluegill (C) collected in Keeler Bay, Lake Champlain in 2018-2019. Dots represent outliers that are 1.5* interquartile range. Note, horizontal lines that are not within a boxplot are single fish rather than mean values.
Fig. 2.12: Bioenergetics model results for yellow perch (A), pumpkinseed (B), and bluegill (C) of daily specific rates measured in joules/gram of fish/day. Values are monthly averages of daily specific consumption, metabolic, and growth rates. $M = R + SDA$. Error bars represent the standard deviation surrounding the monthly mean. Dashed line at $y=0$ used to highlight negative rates. Growth rates represent the assimilated energy allocated to both somatic and gonadal growth.
Fig. 2.13: Seasonal variations in the ratio of metabolic costs (daily metabolic rates) to energy consumption (M/C) for yellow perch (A), pumpkinseed (B), and bluegill (C). \( M = R + SDA \). Values are monthly averages of \( M/C \). Dashed line at \( y=1 \) used to highlight when metabolic costs equal energy consumption. Error bars represent the standard deviation surrounding the monthly mean.
CHAPTER 3: BIBLIOGRAPHY


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### APPENDIX

Table A.1: Conversions from length to wet mass for taxa found in fish stomachs. L = prey item length in mm. For Amphipoda, Asellidae, Trichoptera, Chironomidae, and Gastropoda, M = dry mass in mg. For Copepoda, *Daphnia*, Ostracoda, and other Cladocera, M = dry mass in μg. For fish, M = wet mass in g. Dry weights (DW) are converted to wet weights (WW) using a taxa-specific multiplier.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Equation</th>
<th>DW to WW</th>
<th>Source for length to dry mass</th>
<th>Source for dry to wet mass</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CRUSTACEA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphipoda</td>
<td>$M=0.0058L^{3.015}$</td>
<td>7</td>
<td>Benke et al. 1999</td>
<td>A. Gamble</td>
</tr>
<tr>
<td>Asellidae</td>
<td>$M=0.0054L^{2.948}$</td>
<td>6</td>
<td>Benke et al. 1999</td>
<td>A. Gamble; Sage 1982</td>
</tr>
<tr>
<td>Copepoda</td>
<td>$W=6.03L^{2.744}$</td>
<td>8.33</td>
<td>Gamble 2010</td>
<td>A. Gamble; Downing &amp; Rigler 1984</td>
</tr>
<tr>
<td><em>Daphnia</em> spp.</td>
<td>$M=10.89653L^{2.09955}$</td>
<td>8.33</td>
<td>Gamble 2010</td>
<td>A. Gamble; Downing &amp; Rigler 1984</td>
</tr>
<tr>
<td>Ostracoda (class)</td>
<td>$\log_{10}M=3.24\log_{10}L-3.79$</td>
<td>8.33</td>
<td>Newrkla 1985</td>
<td>A. Gamble; Downing &amp; Rigler 1984</td>
</tr>
<tr>
<td>Other Cladocera</td>
<td>$M=14.9597L^{2.7955}$</td>
<td>8.33</td>
<td>Gamble 2010</td>
<td>A. Gamble; Downing &amp; Rigler 1984</td>
</tr>
<tr>
<td><strong>INSECTA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trichoptera</td>
<td>$M=0.0056L^{2.839}$</td>
<td>2.5</td>
<td>Benke et al. 1999</td>
<td>A. Gamble; Sage 1982</td>
</tr>
<tr>
<td>Chironomidae larvae</td>
<td>$M=0.0059L^{2.099}$</td>
<td>6</td>
<td>Benke et al. 1999</td>
<td>A. Gamble; Sage 1982</td>
</tr>
<tr>
<td>Chironomidae pupae</td>
<td>$M=0.0059L^{2.099}$</td>
<td>2.5</td>
<td>Benke et al. 1999</td>
<td>A. Gamble; Sage 1982</td>
</tr>
<tr>
<td><strong>MOLLUSCA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>$M=0.0331L^{2.851}$</td>
<td>5</td>
<td>Benke et al. 1999</td>
<td>A. Gamble; Ross &amp; Lima 1994</td>
</tr>
<tr>
<td><strong>FISHES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish spp. (unidentified)</td>
<td>$\ln M= -12.2167 + 3.0799 \ln L$</td>
<td>N/A</td>
<td>USGS Lake Superior Biological Station, unpublished data</td>
<td></td>
</tr>
</tbody>
</table>

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Table A.2: Model inputs for yellow perch and sunfish initial and final masses used in bioenergetics modeling. Only age-3 mass inputs were used in the bioenergetics model because the 3-year old age class was most abundant during the study for each species and sample sizes of other ages were too small to populate the model. Mass-at-age data for 2018 and 2019 were combined for these estimates.

| Age | Yellow Perch | | | | Sunfishes | | | |
|-----|--------------|--------|--------|----------|---------|--------|--------|
|     | Initial mass (g) | Final mass (g) | Initial mass (g) | Final mass (g) |
| 2   | 45.8         | 59.2    | 26.0    | 62.2     |
| 3   | 59.2         | 66.9    | 62.2    | 93.3     |
| 4   | 66.9         | 71.9    | 93.3    | 102.3    |

Table A.3: Energetic density in joules per gram wet mass of prey and predator taxon. All data are sourced from Cummins and Wuycheck (1971) except fishes, for which the value was sourced from Pothoven and Höök (2015).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>J/ g WW</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRUSTACEA</td>
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</tr>
<tr>
<td>Amphipoda</td>
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</tr>
<tr>
<td>Asellidae</td>
<td>2095</td>
</tr>
<tr>
<td>Copepoda</td>
<td>2907</td>
</tr>
<tr>
<td><em>Daphnia</em> spp.</td>
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</tr>
<tr>
<td>Ostracoda</td>
<td>2854</td>
</tr>
<tr>
<td>Other Cladocera</td>
<td>2523</td>
</tr>
<tr>
<td>INSECTA</td>
<td></td>
</tr>
<tr>
<td>Trichoptera</td>
<td>8366</td>
</tr>
<tr>
<td>Chironomidae larvae</td>
<td>3610</td>
</tr>
<tr>
<td>Chironomidae pupae</td>
<td>2745</td>
</tr>
<tr>
<td>MOLLUSCA</td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>1799</td>
</tr>
<tr>
<td>FISHES</td>
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<tr>
<td>Other Fish</td>
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Table A.4: Predator energy density values of yellow perch, pumpkinseed, and bluegill used in bioenergetics simulations. Values were calculated as the seasonal average percent dry mass of individuals caught in this study.

<table>
<thead>
<tr>
<th>Day</th>
<th>Yellow Perch Energy Density (J/g wet)</th>
<th>Pumpkinseed Energy Density (J/g wet)</th>
<th>Bluegill Energy Density (J/g wet)</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>5648</td>
<td>6085</td>
<td>1</td>
</tr>
<tr>
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<td>5648</td>
<td>6085</td>
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<td>358</td>
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Table A.5: Water temperature values used for bioenergetics simulations. Temperature data were obtained from the Vermont EPSCoR Data Buoy located in Inner St. Albans Bay, Lake Champlain at an average depth of 3.5 m from September 01 to October 30 in 2018 and June 03 to November 11 in 2019. * denotes when direct surface temperature measurements were used when no Vermont EPSCoR data was available. Water temperatures beneath the ice were modeled to equal 4.0 °C.

<table>
<thead>
<tr>
<th>Yellow Perch</th>
<th>Pumpkinseed and Bluegill</th>
</tr>
</thead>
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<td>Day</td>
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<td>45</td>
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<tr>
<td>384</td>
<td>14.41</td>
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Table A.6: Summary of numerical diet composition by season for three predator species collected in Keeler Bay, Lake Champlain in 2018-2019. BG – bluegill, PS – pumpkinseed, YP – yellow perch. N represents the number of fish caught. Prey item values represent the mean numerical percent diet composition and are abbreviated: Amphi= Amphipoda; Asell= Asellidae; Chiron= Chironomidae; Clad= Cladocera; Cope= Copepoda; Gastro= Gastropoda; Ostra= Ostracoda; Tricho= Trichoptera. AvgH represents the average Shannon’s Diversity Index score (H) and seH represents the standard error H.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>N</th>
<th>% Empty</th>
<th>Amphi</th>
<th>Asell</th>
<th>Chiron</th>
<th>Clad</th>
<th>Cope</th>
<th>Fish</th>
<th>Gastro</th>
<th>Ostra</th>
<th>Other</th>
<th>Tricho</th>
<th>AvgH</th>
<th>seH</th>
</tr>
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<tbody>
<tr>
<td>BG</td>
<td>Autumn 2018</td>
<td>17</td>
<td>6</td>
<td>0.34</td>
<td>0</td>
<td>0.21</td>
<td>0.08</td>
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<td>0</td>
<td>0.04</td>
<td>0.18</td>
<td>0.02</td>
<td>0.1</td>
<td>1.26</td>
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<tr>
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<td>Autumn 2019</td>
<td>31</td>
<td>13</td>
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<td>0</td>
<td>0.26</td>
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<td>0.05</td>
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<td>0.18</td>
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<td>0.29</td>
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<td>0</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td>PS</td>
<td>Summer 2019</td>
<td>51</td>
<td>37</td>
<td>0.23</td>
<td>0.02</td>
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<tr>
<td>Species</td>
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<td>N</td>
<td>% Empty</td>
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<td>Asell</td>
<td>Chiron</td>
<td>Clad</td>
<td>Cope</td>
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<td>Ostra</td>
<td>Other</td>
<td>Tricho</td>
<td>AvgH</td>
<td>seH</td>
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</tr>
<tr>
<td>YP</td>
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