Contributions of winter foraging to the annual growth of thermally dissimilar fish species

Benjamin D. Block · Jason D. Stockwell · J. Ellen Marsden

Abstract The seasonal energy dynamics of temperate fishes will likely be affected by climate change, especially during the winter. Few studies, however, have focused on winter. 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 given expected changes in winter conditions. We used stomach content data, total lipid analyses, and bioenergetics modeling to assess the effects of winter foraging on three species in Lake Champlain, Vermont, USA. We compared 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*). Our results indicate that winter energy dynamics likely depend on the thermal preference of individual fish species – the cool-water species foraged in all seasons whereas the two warm-water species foraged only in the open-

water seasons. In addition, winter foraging provided sufficient energy for overwinter growth in cool-water species but not in warm-water species. Climate change will affect the seasonal energy dynamics that these species have evolved to survive winter conditions in temperate lakes. Thus, we expect climate change to affect individual survival and reproductive success.

Keywords Under ice sampling · Seasonality · Lipids · Bioenergetics modeling · Diet

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Introduction

Fish are more active in winter than previously thought (Shuter et al., 2012). For example, fish actively forage in low water temperatures and under low light conditions (Eloranta et al., 2013; Hayden et al., 2013) and some species may consume large proportions of their yearly energy requirements during winter (Eckmann, 2004; Stockwell et al., 2014). In addition, fish that forage in winter may have seasonally dissimilar diets (Hayden et al., 2013; Anderson et al., 2016). Winter is, however, logistically challenging for fieldwork in temperate freshwater lakes, and consequently, the winter ecology of freshwater fishes has been understudied (Shuter et al., 2012; Fernandes & McMeans, 2019). We have limited knowledge of the relative importance of winter for

fish life history, population dynamics, and overall ecology even though winter conditions have the potential to affect many aspects of fish ecology, including maternal condition, energy allocation, reproductive success, recruitment, and species coexistence (Farmer et al., 2015; McMeans et al., 2020). Consequently, additional studies are needed to evaluate the energetic contributions of winter foraging to the annual growth of freshwater fishes to better understand the potential impacts of changing winter ice phenology (Sharma et al., 2019; Woolway & Merchant, 2019).

The degree to which winter conditions affect the foraging behavior, physiology, and energy dynamics of fish may depend on thermal preferences (Shuter et al., 2012) because fish have enzymatic and physiological specializations that allow them to grow and function optimally within certain temperature ranges (Magnuson et al., 1979; Hasnain et al., 2010). For example, warm-water fish (preferred temperatures > 25°C) are less likely to forage in winter because temperatures are below their preferred range, whereas cold-water fish (preferred temperatures < 19°C) are more likely to forage in winter (Shuter et al., 2012; McMeans et al., 2015). Winter foraging by cool-water fishes (preferred temperatures 19–25°C) is variable (Johnson & Evans, 1991; Shuter et al., 2012), but the conditions under which they forage are unknown. The relationships between thermal preferences and winter foraging patterns stem largely from lab-based studies, although a limited number of in situ studies have tested these relationships (Shuter et al., 2012; Fernandes & McMeans, 2019). Nevertheless, the ability to forage in winter directly affects the seasonal energy dynamics, annual growth, and reproduction of temperate fishes (Byström et al., 2006; Eloranta et al., 2013).

Lower energy consumption and smaller energy reserves in winter compared to other seasons result in less energy available for growth and reproduction (Giacomini & Shuter, 2013; Ejsmond et al., 2015). However, metabolic costs are lower in winter than in other seasons (Clarke & Johnston, 1999; Barneche & Allen, 2018); if fish actively forage in winter, consumed energy may be more efficiently assimilated to growth, reproduction, or storage compared to other seasons. For example, juvenile lake trout *Salvelinus namaycush* in Lake Champlain grow in length and sustain their body condition over winter (Wilkins,

2019), and lake whitefish *Coregonus clupeaformis* in Lake Superior consume 34% of their annual energy consumption and increase lipid content over winter (Stockwell et al., 2014). Also, European whitefish *Coregonus lavaretus* in sub-arctic Lake Kilpisjärvi rapidly increase muscle fatty acids after spawning in winter (Keva et al., 2019). Most research on winter diets and energy consumption, however, has focused on cold-water species and few studies outside of laboratory experiments have focused on cool- or warm-water species.

In this study, we tested whether fish from warm- and cool-water thermal guilds differed in how winter foraging contributed to their seasonal energy dynamics and growth. We used pumpkinseed *Lepomis gibbosus* (Linnaeus) and bluegill *L. macrochirus* (Rafinesque) (collectively "sunfish") as representative warm-water species and yellow perch *Perca flavescens* (Mitchill) as a cool-water species (Hasnain et al., 2010). We hypothesized that yellow perch forage in all seasons whereas sunfish do not forage in the winter, resulting in positive growth in the former and negative growth (mass loss) in the latter over winter. We tested our hypotheses in Lake Champlain using demographic data, stomach content analyses, percent total lipids, 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), relatively shallow (12 m maximum depth) embayment on the eastern side of Grand Isle, VT. 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.). Northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieu*, walleye *Sander vitreus*, fathead minnow *Pimephales promelas,* and bluntnose minnow *P. notatus* are also present in Keeler Bay. Keeler Bay typically has ice cover for 4–5 months, from December until April.

Sample collection

From September 2018 through 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 × 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 h (3 h maximum) to minimize digestion of stomach contents. In winter, fish were angled using ice fishing rods equipped with tungsten jigs (3–4 mm; size 14–16 hooks) and small blow-fly larvae as bait. In all seasons, fish were killed immediately using cranial concussion and put on ice in the field until they were stored in the laboratory at − 20°C.

Laboratory processing

Fish were thawed in the laboratory, and demographic data were recorded (total length, mass, sex, and gonad mass). The age of each fish was estimated from otoliths using the "crack-and-burn" method (Schreiner & 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 and lipid analyses.

Stomachs were removed and stored in 95% ethanol. Stomach 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: Amphipoda (likely Gammaridae), Chironomidae (larvae and pupae), Cladocera, Copepoda, fish, Gastropoda, Isopoda, Ostracoda, Trichoptera, and other invertebrates (crayfish, Bryozoa resting cells, bivalves, damselflies, ephippia, and Hydrachnidia). Prey items labeled "other invertebrates" were relatively rare and appeared in less than 5% of fish collected. In a single fish stomach, the first 20 whole individuals of each

prey taxa were measured; any additional individuals were only enumerated. The longest axis of intact invertebrates was measured to the nearest 10 μm and the total length of intact 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 entire 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. Most fish carcasses ($n = 600/791$ samples) were analyzed for percent total lipid content (PTLC). Samples from 2018 were not analyzed for PTLC. Also, small, young-of-year fish were not included in lipid analyses because the dried samples lacked sufficient mass for replicate analyses.

After stomach and otolith extractions, each thawed fish was homogenized in a NutriBullet Original Blender (600 W) 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 h 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 s using a vortex and centrifuged for 10 min 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 h 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. Total 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 total lipid content for each fish. Standardized total lipid content (STLC) was estimated as the average estimate of total lipid content standardized by fish body mass:

$$\text{STLC} = \frac{\text{Total lipid content(proportion of dry mass)}}{\text{Body mass(g)}}$$

STLC estimates with coefficients of variation greater than 60% were not included in data analyses (yellow perch = 10/346 individuals, pumpkinseed = 4/71 individuals, bluegill = 2/176 individuals).

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

$$K = \left(W/L^3\right) \times 100,$$

where W is the wet mass (g) and L the total length (mm). Population-level seasonal variations in condition and STLC were used to assess seasonal energy fluctuations.

Diet metrics

Diet data from individuals were pooled by season, where season was defined by water temperature in the epilimnion and ice cover: autumn 2018 (open water, temperature < 15°C), winter (ice-covered, temperature < 1°C), spring (open water, temperature < 15°C), summer (open water, temperature > 15°C), and autumn 2019 (open water, temperature < 15°C). 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 prey item using length to dry mass and dry mass to wet mass conversion equations derived from literature sources (Table S1). 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 and biomass. 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, were used to visualize seasonal differences in diet composition and feeding strategy in yellow perch and sunfishes.

Stomach content prey diversity was calculated using the Shannon diversity index (H; Shannon & 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 fish, excluding those with empty stomachs and unidentifiable prey, was assigned a prey diversity score and averaged by season to assess seasonal changes in diet diversity.

Data analysis

Species-specific seasonal differences in the number of prey found in their stomachs were analyzed using Welch's ANOVA and the Kruskal–Wallis H test, depending on data distributions. Subsequent post hoc tests were conducted to determine pairwise differences in diet content among seasons. Yellow perch prey count data were $\log_e$-transformed because residuals were not normally distributed, and a Welch's ANOVA was then used to determine seasonal differences in prey counts. Pairwise t-tests with a Bonferroni correction were then used to evaluate which seasons differed from each other. Pumpkinseed and bluegill prey count data were analyzed using a Kruskal–Wallis H test because the residuals were not normally distributed, but variances were homogeneous among seasons. Pairwise Wilcoxon Rank Sum Tests with a Bonferroni correction were then used to evaluate which seasons differed from each other. Yellow perch and bluegill biomass data were inversely transformed to obtain homogeneity of variances among seasons; however, the residuals remained non-normally distributed. Pumpkinseed biomass data were not transformed because the residuals were not normally distributed, but variances were homogeneous among seasons. Species-specific seasonal differences in the amount of prey biomass found in stomachs were analyzed using the Kruskal–Wallis H test for each of the three species. Pairwise Wilcoxon Rank Sum Tests with a Bonferroni correction were used to evaluate which seasons differed from each other. All analyses were conducted using the R statistical environment (version 3.5.2; R Core Team, 2018).

Schoener's index of percentage overlap (P_{jk}) was used to assess the similarity of diets between seasons (Schoener, 1970). Species-specific seasonal averages of prey counts and prey biomasses were used to calculate the percent overlap index. 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:

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

where p_{ij} is the proportion that prey i is of the total prey found in the stomachs in season j, p_{ik} is the proportion that prey i is of the total prey found in the stomachs 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. Bioenergetics model simulations were performed using Fish Bioenergetics 4.0 (FB4) (Deslauriers et al., 2017). The model was fit to observed annual growth of the 2018 age-3 yellow perch, pumpkinseed, and bluegill cohorts 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. Consumed energy is first allocated to metabolism ($R + A + SDA$), a portion 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).

We modeled bioenergetics of yellow perch and bluegill separately using species-specific parameters 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. Model simulations ran on a daily time step 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 species.

Biological inputs for the bioenergetics model included growth, reproduction, diet composition, and predator and prey energy densities. Biological inputs represented average individuals from each species. Values and data derivations of these inputs are detailed in the Supplementary Material, Tables S1–S5.

Daily lake temperature data were obtained from a sensored buoy located in Inner St. Albans Bay, Lake Champlain (44° 47′ 37.889″ N, 073° 9′ 18.641″ W) 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 S4; Zia et al., 2016). Temperature data were collected every hour and were averaged to estimate average daily temperature. Direct surface temperature measurements, taken using a handheld thermometer in Keeler Bay, were used when buoy temperature data were not available. Surface temperature measurements from Keeler Bay were not significantly different than temperature measurements from Inner St. Albans Bay when observations from both locations were available on the same days (Paired t test, $t_8 = 2.31$, $P = 0.651$).

We assumed that fish behaviorally thermoregulated by occupying habitats in which temperatures are within their preferred temperature range when available (Kao et al., 2015). We used the average optimum growth temperature (OGT) of 25°C for yellow perch and pumpkinseed and an average OGT of 29°C for bluegill (Hasnain et al., 2010). Warm- and cool-water species are also distinguished by other thermal metrics which are not included in our study. When water temperatures were lower than the average OGT, we used the warmest temperature available to approximate the temperature experienced by the modeled fish. In winter, we assumed that the modeled fish occupied 4.0°C.

Daily temperature was modeled as the minimum temperature of ambient water temperature near 3.5 m depth or the average OGT (Kao et al., 2015):

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

where $T_{\exp}(t)$ is the temperature (°C) experienced by the modeled fish on day t, T_{OGT} is the average OGT 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.

Data availability

The datasets are archived at the Forest Ecosystem Monitoring Cooperative (FEMC; https://www.uvm.edu/femc/) at the University of Vermont and are publicly available.

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, and few sunfish ($n = 8$) were caught during this time. Sunfish caught in spring 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 species (Fig. 1, Table S5). The percentage of yellow perch caught with empty stomachs was high in autumn 2018 (39%, total catch = 44) and winter (34%, $n = 122$), and low in spring (8%, $n = 99$) and summer (10%, $n = 77$). Similarly, the percentage of pumpkinseed caught with empty stomachs was highest in winter (76%, $n = 34$) but below 40% in all other seasons. The percentage of bluegill caught with empty stomachs was highest in winter (51%, $n = 124$), and low in autumn 2018 (6%, $n = 17$) and summer (5%, $n = 55$). Thus, all predator populations foraged more frequently in summer and less frequently in autumn and winter.

The average number of diet items and average biomass per stomach varied by season for each predator species (Table 1). The average number of diet items per yellow perch stomach was significantly different among seasons (Welch's ANOVA, $F_{4, 108.61} = 29.717$, $P < 0.001$), with the highest average number of diet items per stomach in summer (528.4–zooplankton dominated, SE = 98.51) and lowest in winter (10.5, SE = 1.50). The average number of diet items per stomach in summer was higher than all other seasons (pairwise t tests, $P < 0.005$) and the average number of diet items per stomach in winter was less than spring ($P < 0.001$). The average biomass per yellow perch stomach was also different among seasons (Kruskal–Wallis H Test, $H = 30.949$, d.f. = 4, $P < 0.001$), with the highest average biomass in autumn 2018 (1,472.8 mg, SE = 335.44) and lowest in autumn 2019 (91.3 mg, SE = 34.25). The average biomass per stomach in autumn 2019 was lower than all other seasons (pairwise Wilcoxon Rank Sum Tests, $P < 0.005$). The average biomass per stomach in autumn 2018 was higher than all other seasons ($P < 0.005$) except summer ($P = 0.08$). Thus, yellow perch had the highest number of prey and the highest biomass per stomach in summer. Note, on average, few prey were consumed in winter yet the average diet biomass was substantial.

The average number of diet items per pumpkinseed stomach was significantly different among seasons (Kruskal–Wallis H Test, $H = 8.541$, d.f. = 3, $P = 0.04$), with 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 only significant inter-seasonal difference in average diet count per stomach occurred between winter and autumn 2018 (pairwise Wilcoxon Rank Sum Tests, $P = 0.005$). The average biomass per pumpkinseed stomach was also different among seasons (Kruskal–Wallis H Test, $H = 10.404$, d.f. = 3, $P = 0.015$), with the highest average biomass in winter (84.2 mg, SE = 27.32) and lowest in autumn 2019 (6.9 mg, SE = 2.26). The average biomass per stomach in winter was higher than autumn 2018 (pairwise Wilcoxon Rank Sum Tests, $P = 0.009$) and autumn 2019 ($P = 0.005$). Thus, pumpkinseed had the fewest number of prey items per stomach, in winter; however, winter prey items had higher biomass than other seasons.

The average number of diet items per bluegill stomach was significantly different among seasons
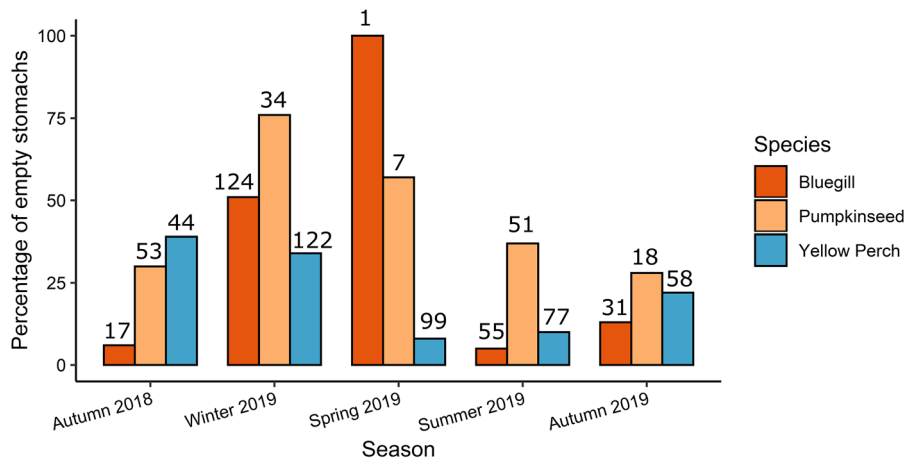
Fig. 1 Percent of fish caught with empty stomachs by season in three fish species collected in Keeler Bay, Lake Champlain in 2018–2019. Values above bars are the total number of fish of a given species caught in each season

Table 1 The average number, average length (mm), average number of prey items per stomach, and average biomass (mg) of prey items per stomach by season for three fish species collected in Keeler Bay, Lake Champlain in 2018–2019

Species	Season	N	Average length	SE	Average # of prey items/stomach	SE	Average biomass/stomach	SE
Bluegill	Autumn 2018	16	139.2	34.6	54.1	11.78	42.5	8.87
Bluegill	Autumn 2019	27	151.9	34.7	29.1	6.40	10.7	2.07
Bluegill	Summer 2019	52	106.6	44.7	152.2	78.19	80.7	26.33
Bluegill	Winter 2019	61	159.6	19.9	9.0	2.55	24.1	4.73
Pumpkinseed	Autumn 2018	37	86.7	28.9	17.0	2.75	18.5	4.31
Pumpkinseed	Autumn 2019	13	120.2	37.9	12.9	5.31	6.9	2.26
Pumpkinseed	Summer 2019	32	115.6	41.4	16.8	4.70	49.9	22.41
Pumpkinseed	Winter 2019	8	164.1	21.0	4.1	1.04	84.2	27.32
Yellow perch	Autumn 2018	27	183.6	37.2	17.7	4.74	1,473.0	335.44
Yellow perch	Autumn 2019	45	186.5	20.6	50.8	8.47	91.3	34.25
Yellow perch	Spring 2019	91	165.1	13.8	60.4	7.57	137.8	29.62
Yellow perch	Summer 2019	69	179.7	17.2	528.0	98.51	219.7	30.97
Yellow perch	Winter 2019	81	172.3	17.3	10.5	1.50	171.3	30.32

N is the total number of fish of a given species caught in each season and SE is the standard error

(Kruskal–Wallis H Test, $H = 62.860$, d.f. = 3, $P < 0.001$), with 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 per stomach was lower in winter than all other seasons (pairwise Wilcoxon Rank Sum Tests, $P < 0.001$). The average biomass per bluegill stomach was also significantly different among seasons (Kruskal–Wallis H Test, $H = 12.786$, d.f. = 3, $P = 0.005$), with the highest

average biomass in summer (80.7 mg, SE = 26.33) and the lowest in winter (24.1 mg, SE = 4.73). The average biomass per stomach in autumn 2018 was different than autumn 2019 (pairwise Wilcoxon Rank Sum Tests, $P < 0.001$) and winter ($P = 0.004$). Thus, bluegill had the highest number of prey and highest biomass per stomach in summer and had the fewest number of prey and small biomass in winter.

Diet composition

Diet composition changed seasonally in terms of prey
count (DC-C) and biomass (DC-B) for each predator
species (Figs. 2, 3). The species richness and diversity
of yellow perch prey was highest in spring (average
Shannon Diversity Score (H) = 0.72, SE = 0.05) and
lowest in autumn 2018 (H = 0.11, SE = 0.05) (Fig. 4,
Table S5). The winter diet of yellow perch was
dominated by isopods and amphipods, and to a lesser
extent, prey fish (Fig. 3). Diets were dominated by
cladocerans in summer, prey fish in autumn 2018, and
chironomids in autumn 2019. Spring diets were
diverse and were not dominated by a single prey
taxon. Prey fish were clustered in the upper left of the
Amundsen plot, which indicates that prey fish are
consumed by a few individuals displaying specializa-
tion (Fig. 3). The majority of prey taxa were low in
prey-specific abundance which indicates that yellow

perch have a generalist feeding strategy throughout all
seasons.

The species richness and diversity of pumpkinseed
prey were highest in autumn 2018 (H = 0.95, SE =
0.06) and lowest in winter (H = 0.17, SE = 0.11)
(Fig. 4, Table S5). Isopods, and to a lesser extent,
chironomids dominated the winter diet of pumpkin-
seed (Fig. 3). 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 (Fig. 3).

The species richness and diversity of bluegill prey
was highest in autumn 2018 (H = 1.26, SE = 0.11)
and lowest in winter (H = 0.29, SE = 0.05) (Fig. 4,
Table S5). The dominant prey taxa of bluegill varied
seasonally (Fig. 3). Isopods, and to a lesser extent,
amphipods and chironomids dominated the diet in
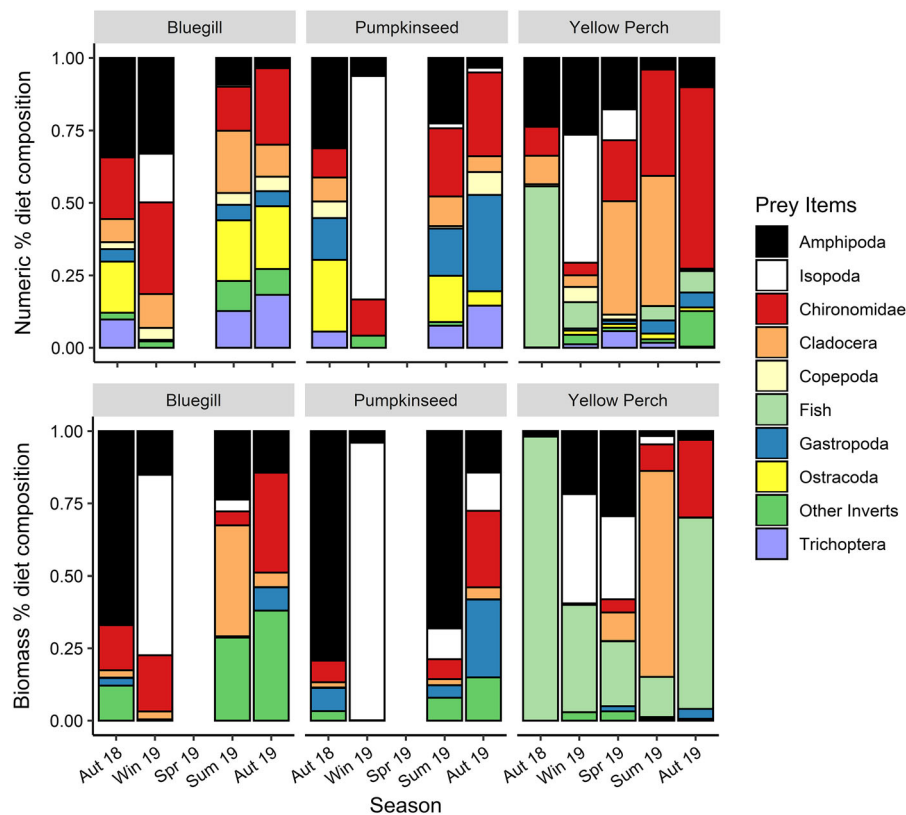winter. Cladocera and Trichoptera were dominant in

Fig. 2 Percent diet composition by prey count and biomass for three fish species collected in Keeler Bay, Lake Champlain in 2018–2019
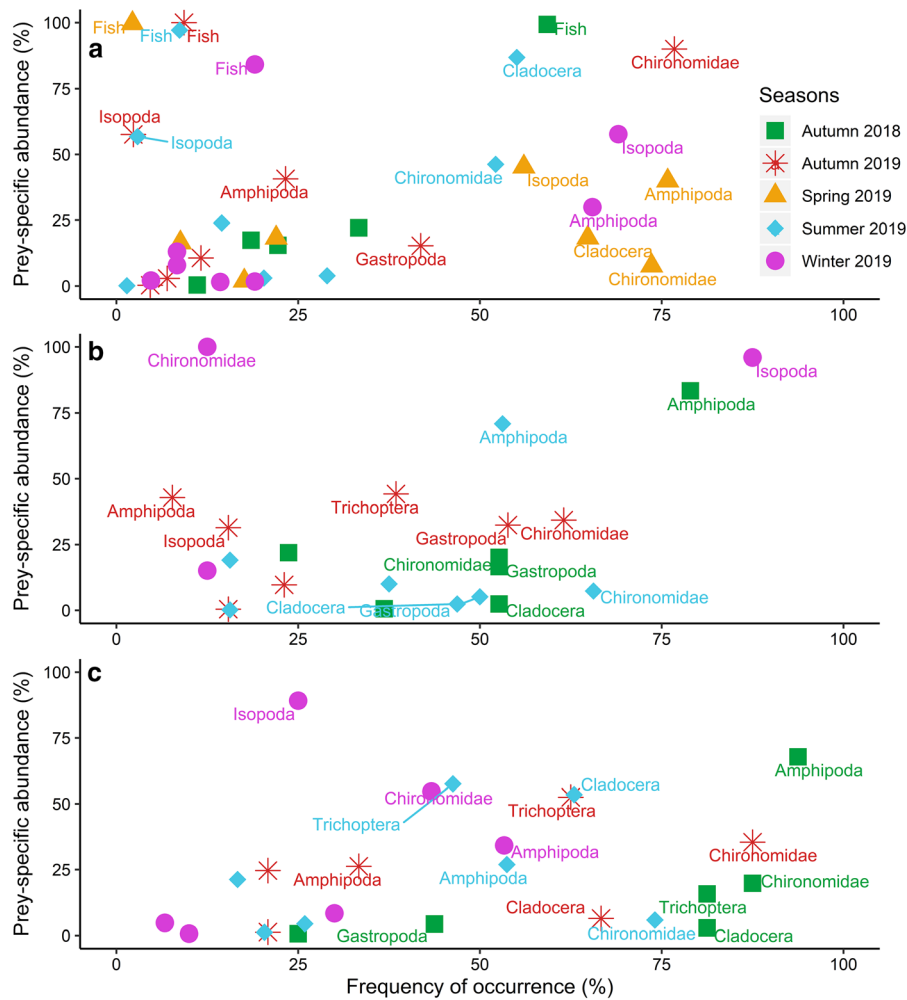
Fig. 3 Seasonal differences in diet composition based on biomass and feeding strategy in yellow perch (A), pumpkinseed (B), and bluegill (C) collected in Keeler Bay, Lake Champlain in 2018-2019. Prey-specific abundance is defined as the percentage of prey taxon biomass which composes total biomass in 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 (Amundsen et al., 1996)

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 (Fig. 3). Bluegill and pumpkinseed diets were dominated by the same prey taxa in winter and autumn.

Seasonal diet overlap

Species-specific seasonal differences in DC-C and DC-B were determined using Schoener's percent overlap index. In yellow perch, the DC-C significantly overlapped between spring and summer 2019

($P_{jk} = 0.74$, Table 2). DC-B significantly overlapped between winter and spring 2019 ($P_{jk} = 0.76$), and autumn 2018 and 2019 ($P_{jk} = 0.68$, Table 2). In pumpkinseed, the DC-C in autumn 2018 significantly overlapped with summer 2019 ($P_{jk} = 0.74$) and autumn 2019 ($P_{jk} = 0.64$, Table 2). Summer and autumn 2019 DC-C also significantly overlapped ($P_{jk} = 0.70$). DC-B significantly overlapped between autumn 2018 and summer 2019 ($P_{jk} = 0.84$, Table 2). In bluegill, no pairwise diet overlap comparisons were significant (Table 2).

DC-C and DC-B significantly overlapped in almost every season between pumpkinseed and bluegill. DC-
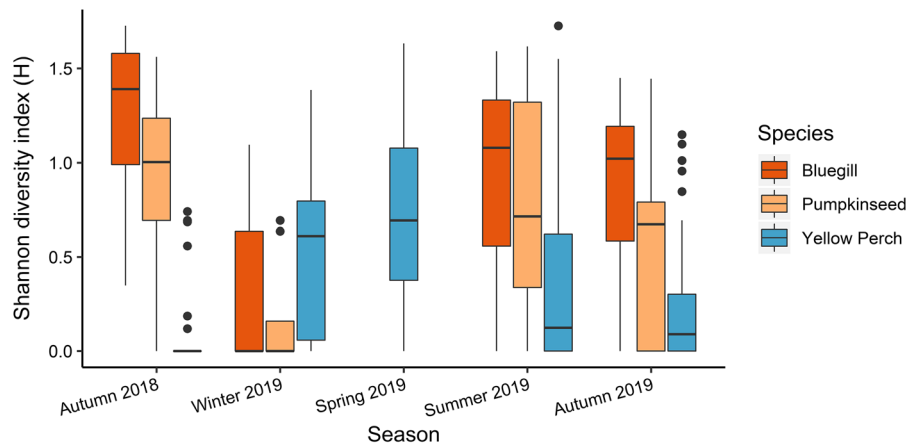
Fig. 4 Seasonal variation in Shannon's diversity index (H) for three fish species collected in Keeler Bay, Lake Champlain in 2018–2019. Dots represent outliers that are 1.5*interquartile range

C of pumpkinseed and bluegill significantly overlapped in autumn 2018 (P_{jk} = 0.80) and 2019 (P_{jk-} = 0.63). DC-B of pumpkinseed and bluegill significantly overlapped in autumn 2018 (P_{jk} = 0.82), winter 2019 (P_{jk} = 0.66), and autumn 2019 (P_{jk-} = 0.68). 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

Standardized total lipid content (STLC) and body condition fluctuated seasonally in all three species. In yellow perch, STLC was highest in July and lowest in March, and highly variable in May, likely around the same time that yellow perch were spawning (Fig. 5). Lipids accumulated from May until July and decreased throughout the late summer and autumn. Late autumn values were similar to values obtained in winter. In pumpkinseed, STLC was lowest in winter and increased in the summer (Fig. 5). The seasonal variation in lipid content in pumpkinseed was similar to the seasonal trend found in yellow perch but lipid content was highest in late summer and autumn. Seasonal and sex-based variation of STLC occurred in bluegill (Fig. 5). 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 STLC in each predator species (Fig. 5). In yellow perch, females often had higher condition than males; however, both sexes followed a similar seasonal pattern. Condition increased through the winter and decreased 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 (GSI) varied seasonally for all three species and showed differences in the timing of gametogenesis (Fig. 5). 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 insufficient pumpkinseed GSI data to observe a trend.

Bioenergetics model simulations

Consumption rates and metabolic rates varied seasonally for each species (Fig. 6). 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. 6). 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

Table 2 Schoener's diet overlap index matrix for yellow perch, pumpkinseed and bluegill based on prey counts and biomass

	Autumn 2018	Winter 2019	Spring 2019	Summer 2019	Autumn 2019
Yellow perch diet overlap based on count					
Autumn 2018	–	0.40	0.31	0.15	0.13
Winter 2019	–	–	0.23	0.11	0.02
Spring 2019	–	–	–	**0.74**	0.15
Summer 2019	–	–	–	–	0.04
Autumn 2019	–	–	–	–	–
Yellow perch diet overlap based on biomass					
Autumn 2018	–	0.39	0.24	0.16	**0.68**
Winter 2019	–	–	**0.76**	0.2	0.41
Spring 2019	–	–	–	0.34	0.33
Summer 2019	–	–	–	–	0.27
Autumn 2019	–	–	–	–	–
Pumpkinseed diet overlap based on count					
Autumn 2018	–	0	NA	**0.74**	**0.64**
Winter 2019	–	–	NA	0.06	0
Spring 2019	–	–	–	NA	NA
Summer 2019	–	–	–	–	0.7
Autumn 2019	–	–	–	–	–
Pumpkinseed diet overlap based on biomass					
Autumn 2018	–	0.04	NA	**0.84**	0.35
Winter 2019	–	–	NA	0.15	0.17
Spring 2019	–	–	–	NA	NA
Summer 2019	–	–	–	–	0.46
Autumn 2019	–	–	–	–	–
Bluegill diet overlap based on count					
Autumn 2018	–	0.41	NA	0.29	0.56
Winter 2019	–	–	NA	0.34	0.38
Spring 2019	–	–	–	NA	NA
Summer 2019	–	–	–	–	0.29
Autumn 2019	–	–	–	–	–
Bluegill diet overlap based on biomass					
Autumn 2018	–	0.34	NA	0.44	0.47
Winter 2019	–	–	NA	0.27	0.37
Spring 2019	–	–	–	NA	NA
Summer 2019	–	–	–	–	0.53
Autumn 2019	–	–	–	–	–

Fish 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) and are shown in boldface. *NA* = insufficient data to calculate index

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, including spring and early autumn. Modeled growth rates were lowest in July which suggests that metabolic costs exceeded energy consumption (Fig. 6). 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. 6). Consumption rates exceeded metabolic rates in all months except February, but M/C varied seasonally (Fig. 6). Unlike yellow perch, pumpkinseed M/C had a unimodal distribution; pumpkinseed M/C increased throughout autumn, had the highest values throughout the winter,
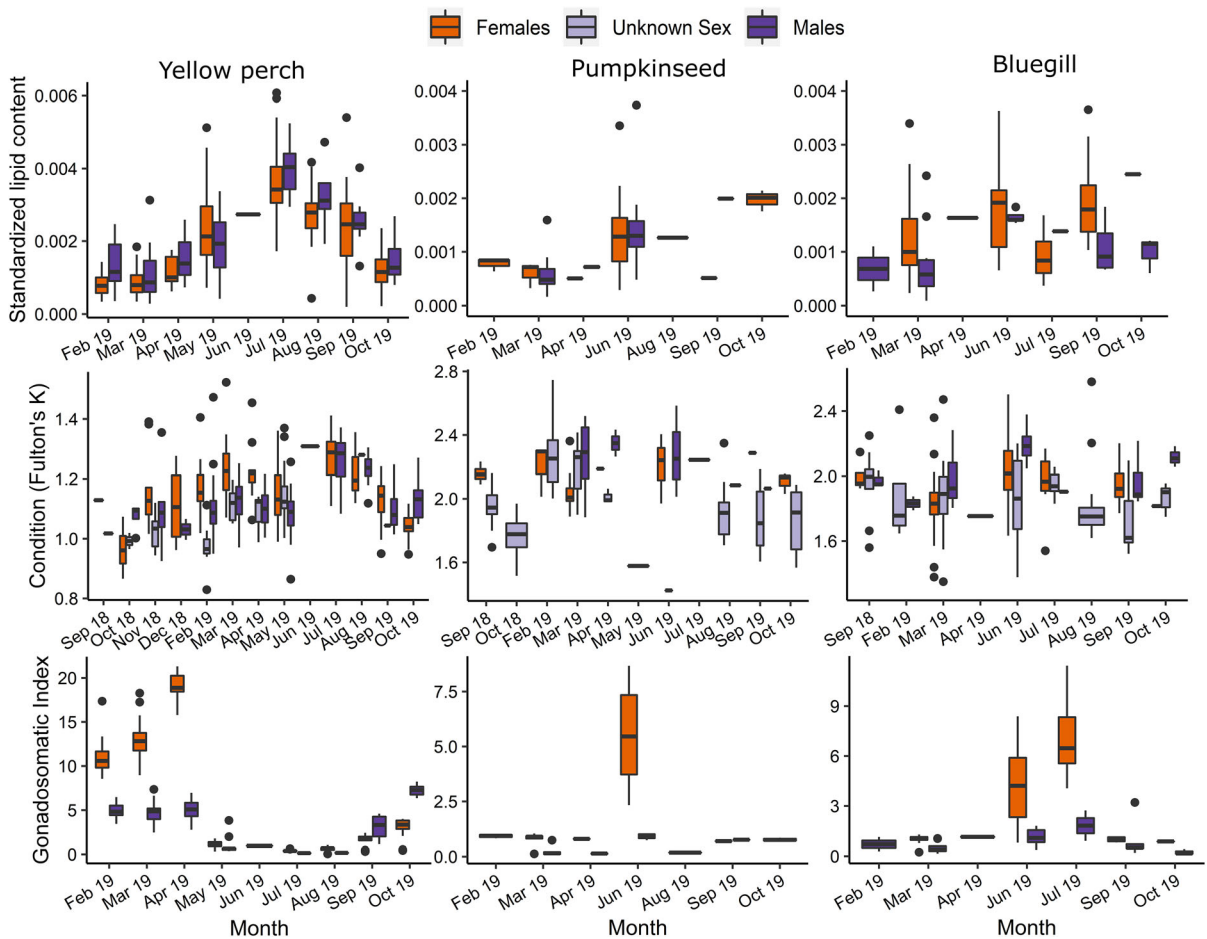
Fig. 5 Standardized total lipid content (total lipid content (proportion of dry mass) per gram of body mass), body condition, and gonadosomatic index by month. Yellow perch, pumpkinseed, and bluegill were collected in Keeler Bay, Lake Champlain in 2019. Dots represent outliers that are beyond the 1.5*interquartile range

and gradually decreased in spring. The lowest M/C occurred in months with high consumption and warm water temperatures. Unlike yellow perch, pumpkinseed modeled growth rates were negative throughout the winter.

Bluegill consumption rates were 17.8 times higher and metabolic rates 6.2 times higher in July than in February (Fig. 6). Consumption rates exceeded metabolic rates in all months except January through March 2019, and M/C varied seasonally (Fig. 6). Similar to pumpkinseed, bluegill M/C had a unimodal distribution; bluegill M/C increased in autumn, peaked in 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 modeled growth rates were

negative throughout the winter and early spring. In combination, the modeling results suggest that in both sunfish species metabolic costs exceeded energy consumption throughout the winter and energy reserves were depleted to meet metabolic demands (Fig. 6).

Discussion

We found that winter foraging behavior and seasonal energy dynamics are strongly influenced by the thermal preference of fish species. Our results support our hypothesis that yellow perch forage in all seasons whereas sunfish forage very little in the winter,
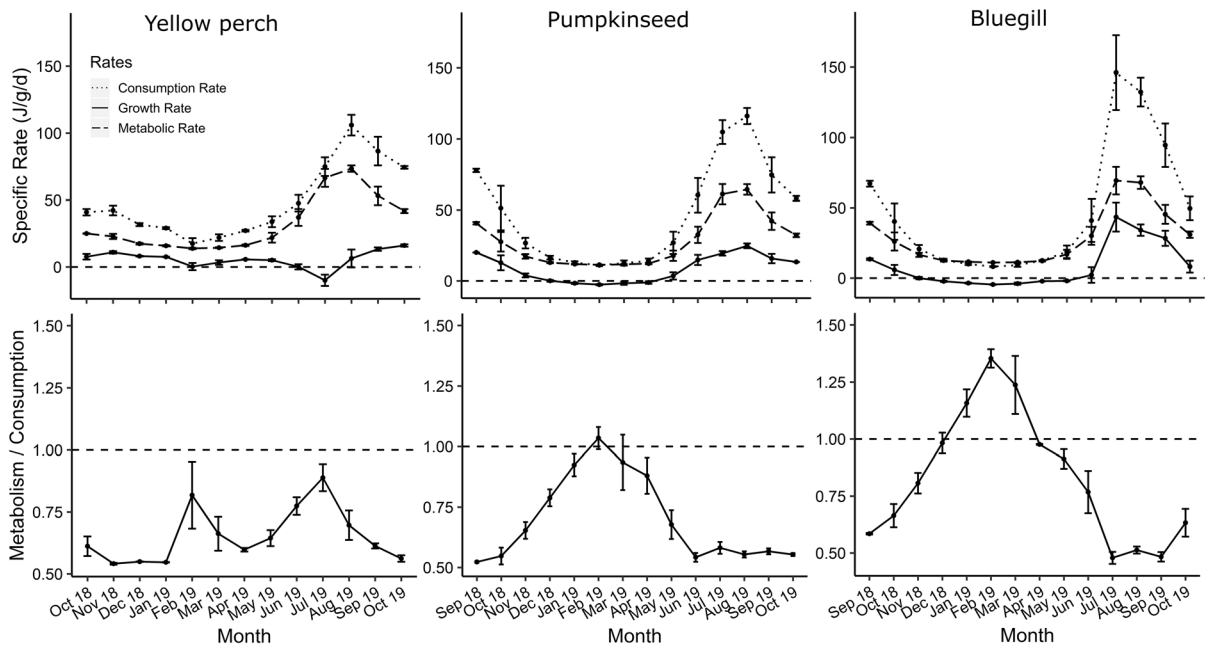
Fig. 6 Bioenergetics model results for yellow perch, pumpkinseed, and bluegill of daily specific rates (joules/gram of fish/day). Top row - monthly averages of daily specific consumption, metabolic, and growth rates. M = R + SDA. Growth rates represent the assimilated energy allocated to both somatic and gonadal growth. Dashed line at y = 0 used to highlight negative rates. Bottom row - monthly averages of M/C. Dashed line at y = 1 indicates when metabolic costs equal energy consumption. Error bars represent the standard deviation around the monthly average

resulting in positive growth in the former and negative growth (mass loss) in the latter over winter.

Each of the three fish species consumed a large variety of prey types, but the species richness and diversity of the diets declined in winter, especially in sunfish, when diets were often dominated by amphipods, chironomids, and isopods. 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 a few taxa. In contrast, the prey diversity of yellow perch in Lake Mendota, Wisconsin decreased from summer to winter (Hasler, 1945). Lake Mendota yellow perch consumed primarily benthic prey in winter, whereas summer diets were more diverse and include pelagic prey. 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 (Mariash et al., 2017).

Seasonality structures food webs by changing the abundance of lower trophic level organisms; therefore, predators such as fish are likely to shift their diets as different prey resources become available throughout the year (McMeans et al., 2015). Seasonal shifts in diet diversity, from surface invertebrates in summer to benthic invertebrates in winter, have been reported in cold-water species such as Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* (Amundsen & Knudsen, 2009). Similarly, Arctic charr in subarctic lakes subsidize their primarily benthivorous diet by consuming zooplankton in winter (Eloranta et al., 2013). Annual changes in the muscle fatty acid composition of European whitefish in subarctic Finland were affected by dietary shifts from benthic macroinvertebrates in winter to zooplankton in summer (Keva et al., 2019). When cisco spawn in early winter 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 available prey likely ensures continued survival in temporally variable food webs and may affect the

transfer of energy and essential fatty acids (McMeans et al., 2015; Keva et al., 2019).

Whether winter prey taxa are targeted due to their relatively high abundances in winter, their ease of capture, or their high lipid content, remains untested and may be a fruitful avenue of future research. Isopods are likely easy to capture, which may explain why they are dominant in the sunfish winter diets. Largemouth bass, a warm-water species, expend more energy when foraging on larger than smaller prey and have been found to preferentially select prey that reduce handling time (Hoyle & Keast, 1987; Selch & Chipps, 2007). Conversely, yellow perch consumed zooplankton and prey fish in winter and did not appear to preferentially select slow-moving prey solely to conserve energy. 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 indicate that winter foraging provides sufficient energy for overwinter growth in yellow perch but not in the sunfishes. Yellow perch in temperate lakes likely use assimilated energy for gametogenesis over the winter (Dabrowski et al., 1996). Modeled growth rates and measured lipid levels of yellow perch were at annual lows in winter; however, GSI increased throughout winter and energy gained in winter may be used in gametogenesis. Female walleye *Sander vitreus* in Lake Erie will forgo spring spawning if sufficient surplus energy reserves are not maintained over winter (Henderson & Nepszy, 1994). Thus, the energy gained and depleted during winter may not only affect individual survival but also future reproductive output and population dynamics (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 through the winter. STLC and body condition of both sunfish species were lowest in winter, and 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 may reduce the rate at which stored energy is depleted in winter by occasionally supplementing energy reserves

(Johnson & Evans, 1991; Speers-Roesch et al., 2018). Unlike yellow perch which spawn soon after ice-out, sunfish in north temperate latitudes do not spawn until June and July and forgo gonad development until ice-out. Warm-water fishes have time between the end of winter and spawning to consume sufficient energy for gonad growth (Giacomini & Shuter, 2013; Ejsmond et al., 2015) as suggested by the energy consumption rates in our bioenergetics models. Thus, warm-water fishes are likely to endure winter and minimize energetic expenditures through prolonged inactivity.

Due to the nature of winter fish work, sample collections and subsequent modeling were limited in several ways. First, prey energy density values used in our models were borrowed from literature sources and do not vary seasonally, a well-known source of error in bioenergetics modeling (Kao et al., 2015; Deslauriers et al., 2017). The use of seasonally variable and site-specific values for prey energy densities is ideal, although these data are costly to obtain. Second, angling is a biased sampling method that may inadvertently have targeted more actively feeding individuals. We used angling because it yielded the highest catch rates. We attempted short-term (3-h) 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; however, larger individuals are likely to move out of Keeler Bay and into the open lake (B. Pientka, VTFWD, pers. comm.), and the size range of fish collected in this study (Table 1) is similar to the size range of fish found in other populations throughout Lake Champlain (Pientka, 2017). Yellow perch (Welch's ANOVA, $F_{4, 151.30} = 17.932$, $P < 0.001$), pumpkinseed ($F_{4, 32.706} = 50.726$, $P < 0.001$), and bluegill ($F_{3, 48.509} = 24.262$, $P < 0.001$) sizes were significantly different among seasons; however, we do not anticipate that seasonal size differences affect foraging because diet composition did not vary by predator length. Ultimately, our results are likely more representative of Keeler Bay rather than Lake Champlain as a whole. Fourth, seasonal habitat use and diet of our study species may have been affected by the presence of predatory fishes which can limit spatial use and affect behavior of prey fish. Therefore, the presence of predatory fishes may affect growth and reproduction more than seasonal variation in abiotic conditions. Results would be expected to vary based on numerous factors including community

composition, lake morphology, ice cover duration, and local temperature regimes.

Winter lake conditions will change due to global climate warming. Average winter water temperatures have increased globally and will likely continue to increase (Gerten & Adrian, 2000; Sharma et al., 2019). 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 (Sharma et al., 2019; Woolway & Merchant, 2019). Thus, climate change is expected to affect fish directly due to temperature and light effects on consumption and metabolism (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 & Johnston, 1999). Increased water temperatures and decreased ice cover have the potential to benefit or harm fish growth, depending on the availability of food (Byström et al., 2006; Brodersen et al., 2011).

In summary, our results indicate that yellow perch foraged and gained sufficient energy for growth in all seasons whereas sunfish foraged in the open-water seasons and had reduced foraging and no growth in the winter. Winter foraging did occur in both the cool-water (yellow perch) and warm-water (sunfish) thermal guilds, but the energetic outcomes differed. However, our study was limited to a single bay in Lake Champlain and only one cool-water species and two warm-water species; therefore, our results may not apply to other members of these thermal guilds in other locations. 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 survive 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.

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