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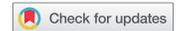
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ARTICLE

Diet Niche Width and Individual Specialization of Brook Trout in Adirondack Lakes

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Abstract

We evaluated diet niche width, individual diet specialization, and diet composition in six lake populations of Brook Trout *Salvelinus fontinalis*, a generalist predator known to exhibit benthic and pelagic trophic specialization. Population diet niche width was broad and similar across all lakes, contrasting with that of individual fish, which exhibited specialized diets in comparison with their population and other individuals. Overall, the degree of individual diet specialization was high compared with that of other fishes. The degree of individual diet specialization did not differ among study populations, although it was generally reduced in spring. Individual diet specialization was consistent across fish sizes despite observed shifts in diet composition with increasing fish length. Population diet composition varied among lakes but was consistent within lakes in all years during the 3-year study period with regard to season and fish size. The consistency and stability in measures of population diet niche width, degree of individual diet specialization, and population diet composition for Brook Trout indicate that these metrics provide useful tools for characterizing fish foraging and measuring how it changes in response to biotic and abiotic perturbations.

Brook Trout *Salvelinus fontinalis* have become a sentinel species for understanding the influence of climate change on coldwater fishes in thousands of north temperate lakes and streams in North America (Warren et al. 2012, 2017; Bassar et al. 2015). These fish are notable for their phenotypic plasticity (Hutchings 1996; Bourke et al. 1997), which allows them to thrive under a wide variety of environmental conditions. As energy acquisition via consumption is key to the growth, reproduction, and survival of all animals, we characterized the plasticity of prey selection by Brook Trout as one component of a broad effort to understand how these and other fishes adapt to variable environments.

Although previous work has shown that Brook Trout consume a broad variety of prey types (Ricker 1932; Carlander 1969; Power 1980)—and thus have been characterized as feeding generalists (Power 1980; Cunjak et al. 1987; Edeline et al. 2013)—individual fish within populations often exhibit substantial variation in their foraging and other behavioral traits (e.g., habitat use, predator avoidance, and mating strategy) (Magurran 1986). Such interindividual variation

influences the life history characteristics and ecological interactions associated with such a widely distributed species (Van Valen 1965; Bolnick et al. 2011). Interindividual variation (also referred to as “individual specialization” [Bolnick et al. 2003; Araújo et al. 2011] or “niche variation” [Van Valen 1965; Bolnick et al. 2007]) in freshwater fish diets has been well documented, but many early studies only investigated the presence or absence of individual variation (Chabot and Maly 1986; Ansaria and Qadri 1989; Beaudoin et al. 1999) and did not address the variation in the degree of individual specialization (Bolnick et al. 2002). More recent approaches have been developed to quantify niche width and the degree of individual specialization, both among and within populations (Bolnick et al. 2002; Araújo et al. 2008). Subsequently, several studies have quantified fish population diet characteristics and individual diet specialization to understand the relationship of this variation to ecological mechanisms such as competition, predation, and population responses to environmental perturbation (e.g., Knudsen et al. 2010; Matthews et al. 2010; Pedreschi et al. 2015).

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Brook Trout in their native range have experienced considerable declines due to habitat loss, the introduction of nonnative fishes, overharvest, and more recently, climate change (Hudy et al. 2008). This decline has spurred conservation efforts to protect the remaining stocks (e.g., the Eastern Brook Trout Joint Venture [www.easternbrooktrout.org]). Research efforts have also been conducted to identify the causes of population decline and to predict the impacts of ongoing threats such as climate change (Meisner 1990; Marschall and Crowder 1996; Warren et al. 2012).

Predation, competition, and prey availability are the primary mechanisms by which climate-induced or other novel species interactions may influence Brook Trout populations. Diet niche width and the degree of individual diet specialization can be affected by all of these mechanisms (Svanbäck and Bolnick 2007; Corder 2013; Eloranta et al. 2013) and, in turn, may influence the degree to which these mechanisms alter ecological dynamics (Araújo et al. 2011). Increased diet niche width alleviates intraspecific competition by limiting interaction among conspecifics, and increased individual diet specialization reduces the impact of interspecific competition by reducing the impact of diet overlap with other species so that it only affects a subset of the individuals in the population (Bolnick et al. 2011). Broad diet niche width and increased individual diet specialization can also dampen prey resource oscillations by reducing the intensity of predation on any one prey source (McCann et al. 1998). Thus, diet niche width and the degree of individual specialization can provide information on the strength of competition, predation, and community structure, which together influence how fish respond to changes in these factors.

Considerable research has been conducted on the diet and foraging behavior of Brook Trout. However, studies showing variable habitat use and trophic polymorphism by Brook Trout (Venne and Magnan 1995; Bourke et al. 1997; Dynes et al. 1999) and variable foraging tactics (McLaughlin et al. 1999) motivated us to examine whether these “generalist” predators show individual diet specialization. Population diet niche width and the degree of individual diet specialization provide an approach to characterizing Brook Trout foraging behavior and quantifying the behavioral changes that may occur in response to novel species interactions resulting from the invasion of nonnative fishes and climate-induced shifts in prey availability. We pursued this question by examining the variation in individual Brook Trout diets both within the same population and across populations (and both within and across years) in six lakes differing in biotic and abiotic characteristics.

We hypothesized that population diet niche width and individual diet specialization would differ between lakes due to differences in available prey and fish community composition. We also hypothesized that individual diet specialization would vary temporally due to shifts in the relative abundances of prey types as well as seasonal thermal constraints. Furthermore, we expected that individual diet specialization

within a lake would be greater for larger fish than for smaller fish, given the expectation that larger fish would feed on the highest-quality prey resources to the exclusion or at the expense of smaller conspecifics.

Although diet niche width and individual diet specialization provide quantitative measures of diet variability, these metrics do not describe the type of prey consumed. We therefore also examined the percent contributions of prey types to the diets of the Brook Trout in each population to evaluate the year-to-year consistency of the composition of the population diet both temporally and across a range of fish sizes. We hypothesized that diet composition would be consistent both within sampling periods (due to cyclical shifts in relative abundance or the availability of various prey) and fish size-classes (due to factors such as gape limitation, metabolic needs, and dominance hierarchy). We use the insights gained from examining diet composition to make inferences about the influence of biotic and abiotic factors on observed differences in Brook Trout foraging patterns among lakes.

Methods

Study lakes.—The six study lakes are located in the southwestern Adirondack Mountains of New York State and included East Lake (ETL), Honnedaga Lake (HAL), Lower Sylvan Pond (LSP), Panther Lake (PRL), Rock Lake (RKL), and Wilmurt Lake (WTL) (Figure 1). These lakes exhibit a range of physicochemical and fish community characteristics (Table 1). The Brook Trout populations in these lakes are self-sustaining, although that in one lake (LSP) is supplemented each fall with stocked fingerlings ($n = 480$).

Fish sampling.—Brook Trout in five lakes were primarily captured using gill nets, with some additional fish being collected via angling; boat electrofishing was the primary means of capture in the remaining lake (HAL). Fish were collected approximately monthly from early May through mid-August except at HAL, which was sampled only in late May each year. Sinking, multifilament gill nets (2.5×50.0 m, 38-mm mesh) were set for 0.25–1.67 h at 15 (30 in HAL) randomly selected sites in each lake during each sampling event. Nets were fished along the bottom perpendicular to shore from the 2.5-m contour outward. The boat electrofishing unit used on HAL was powered by a 6,500-W generator and energized by a Smith-Root Type VI-A electrofisher. Sampling was conducted around the entire perimeter of the lake using regularly spaced (25–30-m), perpendicular pull-ins from the 2-m depth contour to shore.

With one exception, the collected fish were immediately euthanized and placed on ice, and their stomach contents were preserved in 95% ethyl alcohol within 8 h of capture. The exception was fish from HAL, whose stomach contents were collected by gastric lavage at the time of capture and immediately preserved in 95% ethyl alcohol. Most diet items were identified and enumerated to the family level, though some

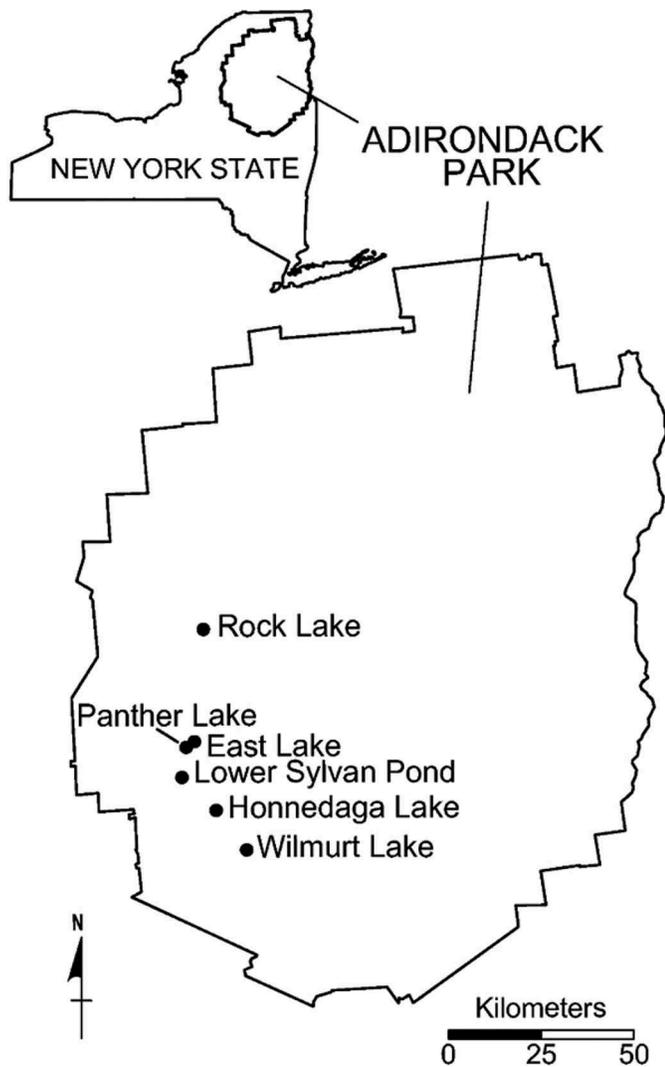


FIGURE 1. Locations of the six lakes within Adirondack Park—East Lake, Honnedaga Lake, Lower Sylvan Pond, Panther Lake, Rock Lake, and Wilmurt Lake—at which Brook Trout diets were characterized in 2008–2010.

taxa (e.g., Ostracoda, Copepoda, and some terrestrial invertebrates) were identified only to order. The taxa that could not be identified to family were rare and were conservatively treated as a single family for the purpose of this investigation. Empty stomachs comprised <3% of the total for all lakes except RKL (7%) and were excluded from the analysis.

Data categorization.—Fish were grouped by total length (<200, 200–249, 250–299, and ≥ 300 mm). These categories were chosen because Brook Trout became susceptible to our gear at approximately 150 mm and showed ontogenetic shifts in diet, including the onset of piscivory, at approximately 200 mm (becoming markedly greater in individuals >300 mm) as well as greater consumption of crayfish (family Cambaridae) beginning at 230–250 mm (Momot 1967; East and Magnan 1991; Robinson 2008). The temporal

composition of Brook Trout diets was assessed by grouping collection dates into three periods. The May–June period included samples collected from early May through mid-June, the time between ice-out and lake stratification. The June–July period included samples collected following thermal stratification. The July–August period included samples collected during the period of greatest thermal stress as hypolimnetic or groundwater refuges diminished in extent.

Total niche width and individual specialization.—We evaluated population diet width and the level of individual diet specialization at the family level (or the lowest level to which prey taxonomy could be determined). The data used for these analyses were expressed as percent contributions to the diet by number. Total niche width (TNW) was used as a measure of population diet niche width (a measure of the richness and abundance of prey types consumed by all individuals sampled) as described and calculated by Bolnick et al. (2002), who developed analytical tools for calculating TNW using diet data expressed as percent contributions by number (or mass).

Total niche width can be divided into two components, the within-individual component (WIC) and the between-individual component (BIC) (Roughgarden 1972; Bolnick et al. 2002). Mathematically,

$$\text{TNW} = \text{WIC} + \text{BIC},$$

where WIC is the average variance of the resources found within individuals' diets and BIC is the variance in mean resource use between individuals. The ratio WIC/TNW provides a measure of specialization by individuals within a population, with interindividual variation (specialization) being high when WIC/TNW is low. We used IndSpec1, a program developed by Bolnick et al. (2002) for analyzing aspects of individual specialization, to calculate WIC, BIC, and TNW. See Bolnick et al. (2002) for details of the derivation and calculation of these measures and access to the IndSpec1 program.

We used multiple measures of individual diet specialization to provide a more robust assessment of this multifaceted trait than can be accomplished using a single metric. Individual diet specialization can be expressed as the variation between an individual and the population or between an individual and other individuals. We therefore calculated the ratio WIC/TNW to provide a measure of the former; interindividual diet variation expressed as E , a measure based on pairwise comparisons of individual diets, was used as a measure of the latter (Araújo et al. 2008). The value of E is calculated by first determining the sample population's overall degree of pairwise overlap of resource use (O), in this case the consumption of specific diet items. The variable O is defined as

$$O = \sum w_{ij},$$

TABLE 1. Physicochemical characteristics and fish community composition of East Lake (ETL), Honnedaga Lake (HAL), Lower Sylvan Pond (LSP), Panther Lake (PRL), Rock Lake (RKL), and Wilmut Lake (WTL). Water chemistry parameters (except pH) represent the means of integrated-depth samples from July through August in the most recent year available (2005–2007); the pH values represent the means of surface (0.5-m depth) samples from the same period.

Parameter	ETL	HAL	LSP	PRL	RKL	WTL
Morphometry						
Elevation (mean surface level [m])	554	667	622	557	546	752
Surface area (ha)	13.4	330.9	6.5	17.4	78.9	39.0
Watershed area (ha)	226.1	1,066.6	48.6	86.3	^a	272.9
Maximum depth (m)	11.6	58.0	4.6	7.0	5.5	10.7
Mean depth (m)	4.8	^a	2.5	4.1	^a	3.6
Maximum thermocline depth (m)	2.5	7.5	None	None	None	6.5
Dominant substrate(s)	Sand–silt	Rock	Sand–silt	Sand–silt	Rock	Sand–silt
Water chemistry						
pH	6.3	5.3	6.2	6.6	5.9	6.6
Acid-neutralizing capacity ($\mu\text{eq/L}$)	156.2	-0.8	40.6	168.7	28.5	57.3
Dissolved organic carbon ($\mu\text{g/L}$)	3.5	0.5	3.1	2.1	2.4	2.4
Total phosphorus ($\mu\text{g/L}$)	7.7	2.9	7.1	6.4	3.6	5.2
Orthophosphate ($\mu\text{g/L}$)	1.2	2.3	3.9	1.2	0.5	1.1
Nitrate ($\mu\text{g/L}$)	0.22	0.33	0.05	0.12	0.10	0.05
Chlorophyll <i>a</i> ($\mu\text{g/L}$)	1.3	0.2	3.3	0.8	1.2	1.6
Secchi depth (m)	3.75	14.25	3.50	6.00	5.37	6.62
Fish community^b						
Atlantic Salmon <i>Salmo salar</i>			S	S		
Blacknose Dace <i>Rhinichthys atratulus</i>	W					
Brook Trout	W	W	W, S	W	W	W
Creek Chub <i>Semotilus atromaculatus</i>						
Rainbow Smelt <i>Osmerus mordax</i>			W			

^a Not available.

^b W = wild, S = stocked as fingerlings, and blank = not present.

where

$$w_{ij} = 1 - 0.5 \sum_{k=1}^K |p_{ik} - p_{jk}|$$

is a measure of the niche pairwise overlap between individuals i and j , with p_{ik} being the frequency of prey category k in individual i 's diet and p_{jk} the frequency of that category in individual j 's diet. The degree of interindividual niche variation in the sample population is then defined as

$$\tilde{O} = \frac{O}{n(n-1)/2} = 2O/n(n-1),$$

in which n is the number of individuals in the sample population. The index of individual specialization, E , is calculated as

$$E = 1 - \tilde{O},$$

resulting in a value of 0 in the absence of interindividual niche variation (similarity of diets among individuals = 100%) and increasing toward 1 with increasing interindividual variation.

The weighted clustering coefficient C_{ws} was used to assess the strength of linkages in resource use by individuals in a population (Araújo et al. 2008). This coefficient evaluates the strength of niche pairwise overlap between individuals (previously defined as w_{ij}) relative to the degree of interindividual niche variation in the sample population (previously defined as \tilde{O}). Individuals with niche pairwise overlap greater than that exhibited by the overall population represent a group of fish specializing in a distinct type of prey. In populations with individuals selecting prey randomly from the overall population diet, C_{ws} will approach 0, whereas C_{ws} will be positive and tend toward +1 in populations with groups of individuals (clusters) consuming a distinct subset of the population diet. In populations in which individual diet overlap is actually lower than that expected by individuals choosing prey randomly from the overall population diet, C_{ws} will be negative and tend toward -1, indicating that diet variation is taking place at the individual level rather than a group level. See Araújo et al. (2008) for details of the derivation and calculation of C_{ws} .

Finally, proportional similarity (PS_i) was used as a third measure of an individual's degree of specialization based on the comparison of the diet distribution of the individual to that of the population rather than to those of other individuals (Bolnick et al. 2002). This measure varies from 1 (complete overlap of the individual and population diets) to 0 (increasing individual specialization) and is calculated

as the diet overlap between an individual i and the population, namely,

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j),$$

where p_{ij} is the proportion of resource j used by the population that is used by individual i and q_j is the proportion of the j th resource category in the population's niche. For individuals that specialize on a single diet item j , PS_i takes on the value q_j . For individuals that consume resources in direct proportion to the population as a whole, PS_i will equal 1. The measure of individual specialization within the population is the average of individuals' PS_i values.

Calculations of TNW, WIC/TNW, and PS_i were performed using the IndSpec1 program developed by Bolnick et al. (2002) for analyzing aspects of individual specialization. Values of TNW and WIC/TNW were calculated for each year (2008–2010) for each lake. IndSpec1 was used to run a nonparametric bootstrap Monte Carlo procedure on WIC/TNW values for each lake to estimate the probability of the observed WIC/TNW. This process generates null diet matrices drawn from the population distribution (Bolnick et al. 2002); we used 1,000 iterations in the bootstrap analysis to determine whether the WIC/TNW observed for each lake was significantly different from that of a population of generalists sampling randomly from the population's diet. PS_i values were calculated for individual fish, and pooled (2008–2010) PS_i values were evaluated for differences in the degree of individual specialization among lakes, fish length categories within lakes, and sampling periods within lakes.

The DIETA1 program (Araújo et al. 2008) was used to calculate E . After E was calculated, the DIETA1 program was used to run a Monte Carlo simulation to test the null hypothesis that any observed diet variation arose from individuals sampling randomly from the overall population diet distribution. We used 1,000 iterations in the bootstrap analysis to determine whether the value of E observed for each lake was significantly different from the value expected from individuals sampling randomly from the population's diet. The DIETA1 program was also used to assess the degree of diet clustering among individuals within each lake based on the weighted clustering coefficient C_{ws} (Araújo et al. 2008). A Monte Carlo bootstrap analysis with 1,000 iterations was performed to test the null hypothesis that the observed C_{ws} arose from individuals sampling stochastically from a shared distribution (Araújo et al. 2008).

Annual mean values of TNW, WIC/TNW, PS_i , and E were compared among lakes. Values for HAL were excluded from these analyses due to the temporally limited (late-May only) data from this lake. A Shapiro–Wilk test of normality and a Bartlett test for homogeneity of variances were applied to the TNW, WIC/TNW, and E values calculated for each lake each

year, and these measures were found to meet the conditions of normality and homoscedasticity. An ANOVA was used to test for differences in the annual mean values of TNW and WIC/TNW and the three-year mean of E among lakes.

A Shapiro–Wilk test for normality and a Bartlett test for homogeneity of variances were applied to the PS_i values by lake, fish length category within lakes, and sampling period within lakes. The lake PS_i values were not normally distributed or homoscedastic even after log and square-root transformation, so the differences in PS_i among all lakes and individual lakes were analyzed using a Welch's ANOVA and Welch's t -test on ranked data, respectively. Welch's ANOVA was used rather than the nonparametric Kruskal–Wallis test because Welch's ANOVA is not sensitive to deviations from normality, especially with large (>30) sample sizes and performs well (in terms of type I error probability) when the number of groups is small to moderate and the sample sizes are moderate to large (Hartung et al. 2002).

The PS_i values by fish length category within lakes met the condition of homoscedasticity in all lakes but that of normality only in LSP and RKL. Because log and square-root transformation of the data for the other four lakes still did not achieve normality, the differences in PS_i in relation to fish length category were evaluated using an ANOVA for lakes for which PS_i grouped by fish length was normally distributed and a Kruskal–Wallis test for lakes for which PS_i grouped by fish length was not normally distributed. As PS_i grouped by sampling period met the condition of homoscedasticity but not normality in all lakes, a Kruskal–Wallis test was used to test for differences in PS_i in relation to sampling period in each lake. In cases where a Kruskal–Wallis test indicated a significant group effect, differences among individual groups were tested for using a Wilcoxon rank-sum test. The significance of all statistical tests was based on $\alpha = 0.05$.

Diet composition.—The diet composition (type and relative abundance of prey) of each Brook Trout population was used to evaluate the consistency of the population diet both temporally and across a range of Brook Trout sizes and to identify biotic and abiotic factors influencing Brook Trout foraging patterns among lakes. Percent similarity differs from the proportional similarity (PS_i) used to measure individual specialization in that PS_i compares an individual with a population, whereas percent similarity compares two populations with each other. The overall composition of Brook Trout diets in each lake was described by the percent contributions of seven pooled prey categories: aquatic insects, crayfish, other macrocrustaceans (primarily isopods), microcrustaceans, fish, terrestrial invertebrates, and all other prey not included in the preceding categories. These categories were chosen to provide a workable number of categories for analysis while incorporating the major components of Brook Trout diets represented in our data and other studies (Carlander 1969).

The percent contribution by number of these categories was calculated with regard to the previously defined sampling periods and fish length categories for each lake. The percent similarity (Whittaker and Fairbanks 1958) of the contributions of prey categories among years for each sampling period and fish length category was used to evaluate the year-to-year consistency of diet composition within sampling periods and size-classes of fish in each lake:

$$\text{Percent similarity} = 100 - 0.5 \sum |a - b| = \sum \min(a, b),$$

where a is the percentage of a prey category in sample A and b is the percentage of the same prey category in sample B. We considered percent similarities >0.60 as biologically significant based on previous studies of diet overlap (Zaret and Rand 1971; Wallace and Ramsey 1983; Smith et al. 2011).

RESULTS

Sample Summary

The total number of diets analyzed from each lake ranged from 52 for HAL to 141 for PRL (Table 2). The most frequent length category was 200–249 mm for all lakes except HAL, for which the <200-mm category had the largest number of fish. Fish >300 mm were relatively rare in ETL (6% of fish sampled) and LSP (10%) and relatively abundant in HAL (27%), RKL (25%), and WTL (26%).

Total Niche Width and Individual Specialization among Populations

Mean annual TNW was not significantly different among lakes ($F = 1.23$, $df = 4$, $P = 0.36$; Table 3; Figure 2A). Mean annual WIC/TNW was low (indicating substantial individual diet specialization) for all lakes and showed no significant differences among lakes ($F = 2.00$, $df = 4$, $P = 0.17$; Table 3; Figure 2B). The bootstrap analysis showed that WIC/TNW was significantly lower than would be expected of a population of generalists for all lakes in all years ($P < 0.01$).

Mean pooled (2008–2010) proportional similarity ranged from 0.26 for RKL to 0.42 for HAL (Table 3; Figure 2C); PS_i was significantly lower for RKL than for all other lakes ($F = 7.09$, $df = 4$, 291.3 , $P \leq 0.01$). Diet variation among individuals as measured by E was significant (Monte Carlo bootstrap analysis, $P < 0.01$) in all lakes but did not vary significantly among lakes ($F = 1.27$, $df = 4$, 10 , $P = 0.35$ for the five lakes excluding HAL; Table 3; Figure 2D). Honnedaga Lake consistently had the lowest degree of individual specialization, regardless of the measure (WIC/TNW, PS_i , or E) evaluated. The bootstrap analysis of the weighted clustering coefficient indicated no clustering of individuals with respect to diet composition in any of the study lakes ($P < 0.01$); C_{ws} was negative for all lakes (Table 3; Figure 2E).

TABLE 2. Number of Brook Trout diet samples analyzed by sampling period and length category for the six study lakes, 2008–2010. For all lakes, the first value in parentheses is the number collected by gill net. For all lakes except HAL, the second number is the number collected by angling; for HAL, it is the number collected by electrofishing.

Parameter	ETL (<i>n</i> = 118)	HAL (<i>n</i> = 52)	LSP (<i>n</i> = 104)	PRL (<i>n</i> = 141)	RKL (<i>n</i> = 139)	WTL (<i>n</i> = 110)
Sampling period						
May–Jun	68 (68/0)	52 (17/35)	52 (52/0)	66 (66/0)	55 (55/0)	56 (56/0)
Jun–Jul	27 (17/10)		28 (28/0)	40 (35/5)	34 (19/15)	32 (32/0)
Jul–Aug	23 (23/0)		24 (24/0)	35 (35/0)	50 (50/0)	22 (22/0)
Fish length (mm)						
<200	31 (28/3)	19 (2/17)	33 (33/0)	46 (45/1)	13 (13/0)	13 (13/0)
200–249	64 (60/4)	12 (5/7)	48 (48/0)	49 (49/0)	59 (58/1)	38 (38/0)
250–299	16 (13/3)	7 (2/5)	13 (13/0)	20 (20/0)	33 (28/5)	31 (31/0)
≥300	7 (7/0)	14 (8/6)	10 (10/0)	26 (22/4)	34 (25/9)	28 (28/0)
Length range	140–400	130–545	151–367	162–405	161–461	170–376

Individual Specialization within Populations

Significant differences in PS_i were found between sampling periods within ETL, LSP, PRL, and RKL (Table 4). In ETL, PS_i was significantly greater (i.e., individual specialization was lower) in May–June than in June–July ($W = 1,275$, $P < 0.01$) and significantly greater in July–August than in May–June ($W = 527$, $P < 0.02$) and June–July ($W = 110$, $P < 0.01$). The value of PS_i was significantly greater in May–June than in June–July and July–August in LSP ($W = 997$, $P < 0.01$ and $W = 898$, $P < 0.01$, respectively) and in PRL ($W = 1,754$, $P < 0.01$ and $W = 1,769$, $P < 0.01$, respectively). In RKL, PS_i was significantly greater in May–June than in July–August ($W = 1,763$, $P = 0.01$). The only lake for which PS_i did not differ significantly between at least two sampling periods was WTL. In contrast, no significant relationships were found between PS_i and fish length-group within any lake (Table 4).

Diet Composition

Seventy-eight taxa were identified from diets examined during this study (see Table A.1 in the appendix to this article). The ETL diets contained the most taxa ($n = 60$), and

the HAL diets contained the fewest ($n = 34$). Twelve taxa were common to all lakes, whereas 17 taxa were found in only one of the six lakes. Seven of these were found only in HAL, five only in ETL, two only in RKL, and one each only in PRL, WTL, and LSP.

The percent contributions of the general prey categories by sampling period varied considerably among lakes (see the Supplement available in the online version of this article, particularly Figure S.1). Comparisons of the percent similarities of the contributions of prey categories to the population diet by sampling period showed significant overlap (mean similarity > 0.60) for all sampling periods in ETL, HAL, LSP, and WTL, two of the three periods in PRL, and only one period in RKL (Table 5). Year-to-year variation in the contributions of prey categories by sampling period was generally lowest in May–June and highest in July–August, though RKL was an exception, exhibiting the opposite pattern.

The influence of fish size on prey consumed varied considerably among lakes (Figure S.2), but 75% (18 of 24) of the comparisons within length-groups showed significant overlap (>0.60 similarity) in the percent contribution of prey types

TABLE 3. Mean annual values for total niche width (TNW), the ratio of the within-individual component to TNW (WIC/TNW), interindividual variation (E), the weighted clustering coefficient (C_{ws}), the 3-year mean for individual proportional similarity (PS_i), the number of items per Brook Trout diet, and number of taxa per diet for the six study lakes. Larger values for WIC/TNW and PS_i and smaller values for E indicate lower degrees of individual diet specialization. The values in parentheses are SEs.

Parameter	ETL	HAL	LSP	PRL	RKL	WTL
TNW	1.21 (0.22)	1.24 (0.38)	1.48 (0.26)	1.25 (0.08)	1.32 (0.36)	0.80 (0.11)
WIC/TNW	0.26 (0.04)	0.49 (0.07)	0.24 (0.04)	0.22 (0.04)	0.30 (0.02)	0.34 (0.04)
E	0.72 (0.02)	0.65 (0.04)	0.79 (0.01)	0.77 (0.02)	0.76 (0.03)	0.73 (0.04)
C_{ws}	−0.16 (0.02)	−0.08 (0.02)	−0.07 (0.03)	−0.21 (0.03)	−0.15 (0.03)	−0.17 (0.04)
PS_i	0.33 (0.08)	0.42 (0.09)	0.31 (0.09)	0.31 (0.07)	0.26 (0.07)	0.34 (0.09)
No./diet	257.0 (32.8)	99.2 (16.4)	77.9 (20.4)	415.6 (50.6)	295.0 (39.0)	379.2 (51.4)
Taxa/diet	5.0 (0.3)	5.2 (0.4)	4.3 (0.2)	4.6 (0.2)	4.9 (0.2)	5.8 (0.3)

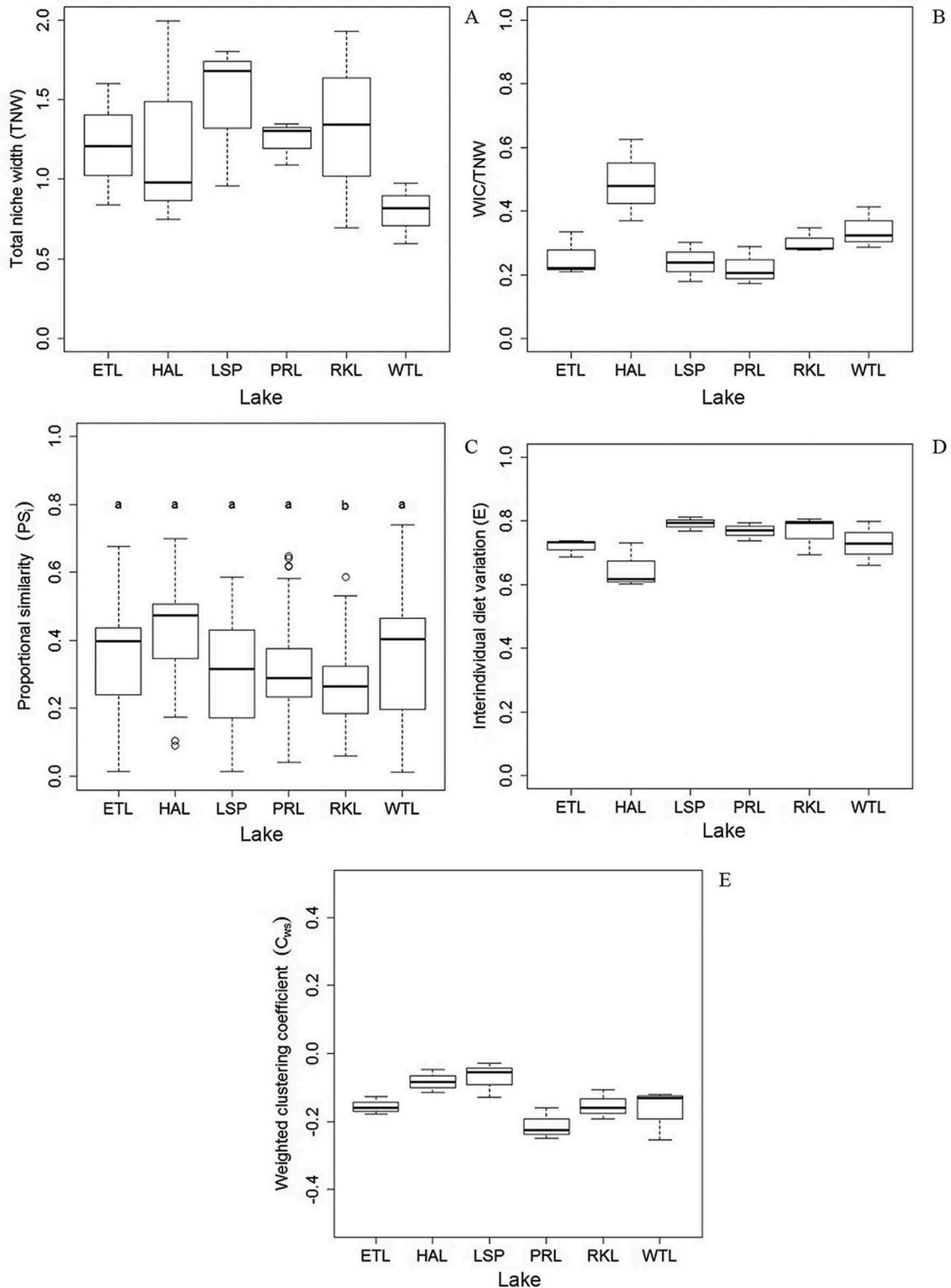


FIGURE 2. Measures of (A) annual population diet niche width (TNW), (B) annual proportion of the within-individual component (WIC) of diet variation to TNW, (C) 3-year mean proportional similarity of individual diets to the population diet (PS_i), (D) annual interindividual variation in diet (E), and (E) annual weighted clustering coefficient (C_{ws}) of diets for Brook Trout from East Lake (ETL), Honnedaga Lake (HAL), Lower Sylvan Pond (LSP), Panther Lake (PRL), Rock Lake (RKL), and Wilmurt Lake (WTL) in 2008–2010. In each box the dark midline represents the median and the lower and upper lines represent the 25th and 75th percentiles, respectively. The whiskers extend up to 1.5 times the interquartile range from the bottom (top) of the box to the furthest datum within that distance. Data points beyond that distance are outliers represented individually as empty circles. Larger values of TNW indicate broader population diet niches. Larger values of WIC/TNW and PS_i indicate lower degrees of individual specialization. Larger values of E indicate higher degrees of individual specialization. Negative values of C_{ws} indicate a lack of clustering (diet specialization is occurring at the individual rather than the group level). Different lowercase letters in panel (C) indicate significant differences among lakes.

TABLE 4. Test statistics, degrees of freedom, and *P*-values for statistical analyses comparing the proportional similarity (*PS*) of Brook Trout diets among fish size categories and sampling periods within study lakes, 2008–2010.

Statistic	Lake					
	ETL	HAL	LSP	PRL	RKL	WTL
By fish size category						
χ^2	4.49	4.04		1.19		0.26
<i>F</i>			2.69		0.88	
df	3	3	3, 28.5	3	3, 45.7	3
<i>P</i>	0.21	0.26	0.06	0.76	0.46	0.97
By sampling period						
χ^2	17.67	^a	13.31	21.74	6.12	1.12
df	2	^a	2	2	2	2
<i>P</i>	<0.01	^a	<0.01	<0.01	0.05	0.57

^a Excluded from this analysis due to temporally limited data.

among years (Table 5). Three of the six instances of nonsignificant overlap were associated with Brook Trout ≥ 300 mm (in ETL, HAL, and LSP); in all three cases, sample size was two or fewer fish for at least one of the three years compared. Brook Trout ≥ 300 mm in PRL, RKL, and WTL had minimum sample sizes of seven or more fish for each year and showed relatively high (72–89%) and significant overlap in diet composition from year to year.

DISCUSSION

Contrary to our expectation, TNW and WIC/TNW were not significantly different among lakes with substantially different physicochemical conditions, fish community characteristics, and forage bases (based on the types and relative abundances of prey items found in the diets). We expected to see differences in TNW among lakes with different prey bases due to the differing abundances of various prey across lakes and a resultant differential expression of the within-individual component (WIC) of TNW. Because the desirability of a prey type should influence how likely consumers are to use alternative prey sources (Bolnick et al. 2010), WIC should differ among populations with different abundances and types of prey. Although we observed substantial differences in the consumption of certain prey taxa (e.g., isopods) among lakes, the diversity of prey consumed did not differ. Furthermore, individual diet specialization as measured by WIC/TNW did not differ significantly among lakes, indicating that the within-individual and between-individual components of diet niche width were similar among populations.

The low WIC/TNW values observed in all of the study lakes indicate that individual fish consumed relatively small components of the overall population diet and that the individuals within each lake had little diet overlap (Bolnick et al. 2003). Similarly, individual diet specialization (indicated by *PS_i* and *E*) reflected low individual diet overlap (high individual specialization) and did not differ among the five lakes with seasonal (spring and summer) diet information. Individual specialization was consistently lower in HAL

TABLE 5. Mean percent similarity of Brook Trout diets by sampling period and fish length category based on the contributions of prey categories for the six study lakes, 2008–2010. Similarity values >0.60 are considered biologically significant. The values in parentheses are SEs. The ranges of *N*-values in the lower portion of the table are the ranges of sample sizes for the three study years.

Parameter	ETL (<i>n</i> = 118)	HAL (<i>n</i> = 52)	LSP (<i>n</i> = 104)	PRL (<i>n</i> = 141)	RKL (<i>n</i> = 139)	WTL (<i>n</i> = 110)
Sampling period						
May–Jun	0.80 (0.03)	0.74 (0.09)	0.84 (0.05)	0.82 (0.04)	0.48 (0.18)	0.76 (0.07)
Jun–Jul	0.80 (0.05)		0.66 (0.11)	0.81 (0.05)	0.56 (0.14)	0.96 (0.01)
Jul–Aug	0.64 (0.08)		0.61 (0.09)	0.29 (0.19)	0.72 (0.07)	0.60 (0.18)
Fish length (mm)						
<200	0.70 (0.07) <i>N</i> = 7–16	0.68 (0.06) <i>N</i> = 1–10	0.81 (0.04) <i>N</i> = 6–16	0.77 (0.01) <i>N</i> = 12–19	0.45 ^a <i>N</i> = 5–8	0.40 (0.19) <i>N</i> = 3–6
200–249	0.85 (0.03) <i>N</i> = 20–27	0.85 (0.04) <i>N</i> = 3–5	0.85 (0.06) <i>N</i> = 12–19	0.78 (0.05) <i>N</i> = 14–21	0.78 (0.08) <i>N</i> = 7–32	0.75 (0.05) <i>N</i> = 10–16
250–299	0.67 (0.08) <i>N</i> = 3–7	0.51 (0.12) <i>N</i> = 1–3	0.72 (0.02) <i>N</i> = 3–6	0.81 (0.06) <i>N</i> = 3–11	0.80 (0.04) <i>N</i> = 6–14	0.93 (0.01) <i>N</i> = 6–17
≥ 300	0.55 (0.07) <i>N</i> = 2–3	0.40 (0.22) <i>N</i> = 1–7	0.25 (0.22) <i>N</i> = 2–4	0.80 (0.05) <i>N</i> = 4–14	0.72 ^b <i>N</i> = 7–27	0.89 (0.04) <i>N</i> = 7–11

^a No fish <200 mm were collected from RKL in 2009; the value reported represents the similarity between 2008 and 2010.

^b No fish ≥ 300 mm were collected from RKL in 2008; the value reported represents the similarity between 2009 and 2010.

regardless of the measure (WIC/TNW, PS_i , or E) evaluated. This likely reflects the availability of HAL diets from only the May–June period, in which individual specialization for the other five lakes was always lower than the annual mean. The lack of differences in total diet niche width and the degree of individual diet specialization among lakes reflect the generalist feeding strategy of Brook Trout at the population level, as documented in previous studies (Power 1980; Cunjak et al. 1987). Yet our results show that the availability of diverse prey evident in TNW provided an opportunity for consistent diet specialization by individual fish.

The consistency in total diet niche width and the degree of individual diet specialization among lakes with differing fish communities were also unexpected. Although we did not examine the diets of sympatric species, the species present in some lakes (Rainbow Smelt, Atlantic Salmon, and Creek Chub) would likely compete with Brook Trout for some available prey (Scott and Crossman 1973). For example, Magnan and FitzGerald (1982) and Magnan (1988) found that Brook Trout living in sympatry with Creek Chub fed mainly on zooplankton whereas allopatric populations of Brook Trout fed primarily on benthic macroinvertebrates. We speculate that the lack of influence of other fishes on Brook Trout population diet niche width and individual diet specialization indicate limited competition between species. Individual specialization should be most evident in environments with limited competition, declining as interspecific competition restricts access to the full range of prey types (Araújo et al. 2011). Although Rainbow Smelt feed primarily on zooplankton and Diptera larvae and pupae (Evans and Loftus 1987), both of these groups still comprised a large component of Brook Trout diets in the two study lakes containing Rainbow Smelt. However, the zooplankton consumed by Brook Trout in one of these lakes (ETL) were primarily small benthic forms instead of the larger pelagic forms consumed in the other lakes. Similarly, Creek Chub and Atlantic Salmon likely compete with Brook Trout for benthic macroinvertebrate prey, yet benthic macroinvertebrates still comprised at least 50% of Brook Trout diets when Brook Trout were sympatric with these species.

As we expected, the degree of individual diet specialization showed significant temporal variation in most (four of the five) lakes sampled over multiple periods. With the exception of the lake with no significant temporal variation, individual specialization was lower in May–June than in June–July and/or July–August, depending on the lake. Temporal differences in individual specialization likely resulted from the interplay of the changing availability of prey resources and the changing intensity of intraspecific and (in the case of ETL) interspecific competition (Araújo et al. 2011). Foraging theory suggests that an expanded prey base, along with greater intraspecific competition, should lead to greater individual specialization due to individual differences in prey preferences, optimization criteria, physiological requirements, and even social hierarchy (Schoener 1971; Stephens and Krebs 1986; Araújo et al.

2011). However, seasonal variations in the abundance of preferred prey could lead to a temporary decline in specialization if individuals converge on seasonally abundant preferred prey.

Brook Trout diets in May–June were dominated by aquatic insects or isopods; the predominance of these groups tended to decline with increasing zooplankton contributions in June–July and, to a lesser extent, in July–August. The timing of this shift coincides with higher littoral zone temperatures that are suboptimal for Brook Trout growth as well as with seasonal increases in zooplankton abundance (Schindler and Novén 1971). In the May–June period, Brook Trout were able to feed freely throughout the littoral zone, where lake benthic macroinvertebrate communities reach their maximum density and diversity (Thorpe and Covich 1991; Ward 1992). The shift from aquatic insects to zooplankton may also reflect changing prey availability due to thermal constraints.

The lack of a significant relationship between individual diet specialization and fish length was unexpected, considering that shifts in diet composition were apparent with increasing fish length and Brook Trout have shown ontogenetic shifts in prey consumption (East and Magnan 1991; Robinson 2008). Larger fish ate fewer zooplankton in all lakes, and isopods and Rainbow Smelt were more abundant in the diets of large Brook Trout in lakes that contained these taxa. Despite observed changes in diet composition with increasing length, the degree of individual diet specialization did not differ over the size range of the fish studied. In another study of individual diet specialization in relation to fish length, Ingram et al. (2011) found that the body size of Threespine Stickleback *Gasterosteus aculeatus* was correlated with prey size and composition but that body size had no effect on the degree of diet variation among individuals. These authors concluded that unless an observed correlation between morphology and diet is very strong, ecological variation among individuals may be largely decoupled from morphological variation. Our findings support this and indicate that although the diet composition of the Brook Trout in our lakes changed as fish increased in size, the overall degree of overlap in their diet—in comparison with that of other individuals—did not change appreciably.

Our observations of individual diet specialization by Brook Trout are consistent with studies showing that generalist populations of organisms often consist of specialized individuals (Araújo et al. 2011). Araújo et al. (2011) reported an average of 51% mean proportional similarity in diet, foraging behavior, or habitat use by 52 species of fish, with an overall range from 20% to 90% (Araújo et al. 2011). More recent studies have reported mean similarities of the diets of individuals to that of the overall population ranging from 25% to 93% (Araújo et al. 2014; Sharp and Chapman 2014; Pedreschi et al. 2015). The Brook Trout in our study lakes exhibited a mean proportional similarity of diets at the low end of that range (26–42%), reflecting a high degree of individual diet specialization. Only one previous study quantified and compared individual diet specialization across multiple

populations of a fish species (Sharp and Chapman 2014). By contrast with our results, that study found that both population diet niche width and the degree of individual diet specialization varied significantly among eight populations of the African cyprinid *Rastrineobola argentea* (also known as *Engraulicypris argentea*) in lakes with different histories of invasion by Nile Perch *Lates niloticus*, yet the differences in diet characteristics were not influenced by the timing of the invasions.

Some reported cases of individual diet specialization in fish have been attributed to morphological or behavioral differences within the population that resulted in subsets of the population clustering their use of forage resources (Bourke et al. 1997; Svanbäck and Bolnick 2007; Knudsen et al. 2010). The Brook Trout in all of the study lakes consistently showed no clustering with respect to diet composition (C_{wvs} was negative for all lakes). Instead, individual diets in each lake were overdispersed, with individual fish consuming combinations of prey that differed from those consumed by other individuals (Araújo et al. 2008). The lack of diet clustering in our study populations suggests that the relatively high level of individual specialization observed was not due to the expression of the distinct morphological or behavioral phenotypes that have been identified in previous studies of diet specialization in *Salvelinus* species (Bourke et al. 1997; Knudsen et al. 2010).

As expected, we found consistent overlap in diet composition within sampling periods in most lakes (there was one exception). This suggests that the composition of Brook Trout diets in spring and summer is consistent seasonally from year to year in the absence of perturbations that affect prey resources or Brook Trout's access to them. The annual consistency of diet composition within fish size-classes was also significant in nearly all (90%) cases where the sample size was three or greater. The consistency of diet composition within sampling periods and fish size-classes over a 3-year period shows that diet data from samples collected in a given period and for a given fish size can be assumed to represent those of other years from the same period, assuming that there are no large-scale perturbations to the food web. This long-term consistency in diet structure has not previously been reported for Brook Trout.

We suspect that some of the differences in diet composition among the study lakes resulted from the presence or absence of specific prey. For example, the presence of isopods in two lakes, Rainbow Smelt in one lake, and crayfish in two others meant that in those lakes there were energy-rich prey not available in other lakes. We speculate that competition with Rainbow Smelt for zooplankton prey in one lake contributed to differences in the composition of zooplankton consumed by the Brook Trout in that lake. Previous studies report that Brook Trout shifted from primarily benthic prey to pelagic prey in response to the presence of a competing benthivore

(Magnan 1988; Lacasse and Magnan 1992; Brown and Rasmussen 2009). Yet we observed the opposite effect, with Brook Trout feeding primarily on benthic zooplankton in sympatry with a competing pelagic planktivore.

We noted differences in Brook Trout diet composition between stratified and unstratified lakes, which indicates the influence of thermal effects on diet. Two of our study lakes are strongly stratified during summer, and the fish in both lakes showed a large increase in the percent contribution of zooplankton in their diet from spring to summer. This coincided with the development of the thermocline in these lakes, a condition that reduces the amount of suitable habitat and consequently the availability of benthic prey. The predominance of zooplankton in summer Brook Trout diets in thermally stratified lakes has been reported by others (Christensen and Moore 2008). Stressful thermal conditions above the thermocline in stratified lakes and throughout unstratified lakes in summer may prevent Brook Trout from foraging in areas with their preferred prey or severely limit their foraging in such areas (Robinson et al. 2010).

Our analysis of individual specialization was based on single-point-in-time observations of diets from individual fish. Studies that have examined the diet consistency of individual fish are rare but suggest that individual fish maintain consistent foraging habits. Largemouth Bass *Micropterus salmoides* showed high diet consistency among individual fish collected in the same year (Schindler et al. 1997). The diets of individual stream-dwelling Brook Trout, Rainbow Trout *Oncorhynchus mykiss*, and Cutthroat Trout *Oncorhynchus clarkii* sampled multiple times (maximum between-sample interval = 21 d, mean = 11.4 d) showed persistent levels of diet specialization in comparison with the diets of other individuals from the same species (Bryan and Larkin 1972). These studies—along with the consistency and prevalence of specialization observed both within and across populations and sampling periods—suggest that individual diet specialization in Brook Trout is not a short-lived phenomenon.

Overall, population diet niche width and the degree of individual diet specialization were consistent across Brook Trout populations despite between-lake differences in the available forage base, the presence of competing species, and physical and thermal characteristics. Brook Trout consumed a broad array of prey at the population level, yet individuals were highly specialized in their individual foraging habits. The degree of individual specialization tended to vary seasonally (spring versus summer) within lakes, and the nature of this variation was similar across lakes. The degree of individual specialization was also consistent across fish sizes despite observed shifts in diet composition with increasing fish length in all lakes.

The consistency of our findings across lakes and time indicates that individual diet specialization by Brook Trout is relatively high in comparison to that reported for other fishes and that it is stable across years. This consistency also suggests that these measures provide useful tools for characterizing Brook Trout foraging behavior and measuring how this behavior changes in response to

environmental perturbations. The extent of competition and predation risk from other fishes in our study lakes was relatively low and the watersheds of these lakes are relatively undisturbed, which may contribute to the observed stability in Brook Trout diet specialization. Future investigations should consider how factors such as more intense competition, the presence of predatory and nonnative fishes, and climate-induced shifts in prey availability and fish community structure affect Brook Trout diet specialization. This may provide a quantifiable measure of the impact of such perturbations and insights into their ecological consequences. We see this type of analysis as equally applicable to other fish species.

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Appendix: Prey Items in Brook Trout Diets

TABLE A.1. Taxonomic classification and percent of diets containing prey items consumed by Brook Trout collected from East Lake (ETL), Honnedaga Lake (HAL), Lower Sylvan Pond (LSP), Panther Lake (PRL), Rock Lake (RKL), and Wilmurt Lake (WTL) from May through mid-August 2008–2010.

Taxon	ETL	HAL	LSP	PRL	RKL	WTL
Nematoda	13.6			0.7		8.2
Gastropoda						
Basommatophora						
Planorbidae	3.4					
Bivalvia						
Veneroidea						
Pisidiidae	0.8			26.2	0.7	1.8
Oligochaeta	0.8					0.9
Hirudinea						
Arhynchobdellida						
Erpobdellidae	0.8		32.7	1.4	7.9	16.4
Phylactolaemata						
Plumatellida	0.8			8.5		0.9
Arachnida						
Araneae	0.8	9.6	1.0	1.4		
Pseudoscorpiones		3.8				
Trombidiformes						
Arrenuridae	4.2					7.3
Hydrachnidae					1.4	
Hydrodromidae		3.8				1.8
Pionidae	2.5		2.9	5.0	0.7	13.6
Unionicolidae	22.9		2.9	7.8	4.3	10.0
Collembola						
Collembola						
Isotomidae	0.8	1.9	1.0			
Insecta						
Baetidae			10.6	1.4		
Caenidae	0.8			0.7		
Ephemerellidae	5.1	1.9	1.0			
Ephemeridae	11.9				30.9	
Heptageniidae	1.7				3.6	0.9
Leptophlebiidae	18.6	61.5	27.9	12.8	15.8	39.1
Metretopodidae	0.8	1.9		0.7		
Siphonuridae	5.9	1.9	15.4	11.3	6.5	10.0
Odonata						
Aeschnidae	1.7	1.9	3.8	2.1	3.6	10.0
Coenagrionidae	9.3	15.4	27.9	23.4	18.0	31.8
Corduliidae	5.9	5.8	4.8	2.8	4.3	17.3
Gomphidae						20.9
Lestidae	0.8		4.8		0.7	0.9
Libellulidae	21.2	1.9	51.9	31.2	18.7	13.6
Macromiidae		1.9				
Plecoptera						
Capniidae		15.4				
Leuctridae	0.8					

TABLE A.1. Continued.

Taxon	ETL	HAL	LSP	PRL	RKL	WTL
Hemiptera						
Aphididae		1.9				
Cicadellidae	0.8			0.7		0.9
Belostomatidae	0.8					
Corixidae	5.1	1.9	20.2	3.5	73.4	7.3
Gerridae	1.7		1.9			0.9
Notonectidae			1.0		10.1	2.7
Terrestrial Hemiptera	0.8	11.5		1.4		0.9
Megaloptera						
Sialidae	15.3	40.4	1.9	3.5	7.9	28.2
Trichoptera						
Dipseudopsidae	8.5		3.8	7.1		12.7
Hydroptilidae	3.4					0.9
Leptoceridae	10.2		7.7	14.9	2.9	5.5
Limnephilidae	3.4		1.9	0.7		4.5
Molannidae	3.4		1.0		5.0	9.1
Odontoceridae			1.8			
Phryganeidae	18.6	26.9	48.1	18.4	8.6	50.9
Polycentropidae	3.4	15.4		2.8	2.2	2.7
Lepidoptera		5.8	1.0			
Coleoptera						
Dytiscidae	6.8		3.8		6.5	1.8
Elmidae	0.8					0.9
Curculionidae		1.9				
Halplidae	2.5					
Saldidae	0.8					
Scirtidae					0.7	
Staphylinidae	0.8		1.0			
Undetermined terrestrial	12.7	23.1	2.9	5.0	2.2	10.0
Undetermined		3.8		0.7		
Diptera						
Ceratopogonidae	2.5		5.8	4.3	2.2	5.5
Chaoboridae	33.9			12.1	46.0	15.5
Chironomidae	93.2	69.2	67.3	85.8	64.7	72.7
Tipulidae		1.9				
Undetermined terrestrial	5.1	23.1	1.9			2.7
Hymenoptera	0.8	15.4			0.7	0.9
Formicidae	1.7	11.5		2.1	2.9	2.7
Ostracoda	8.5			2.1		
Branchiopoda						
Cladocera						
Chydoridae	35.6	3.8	1.9	20.6	6.5	8.2
Daphnidae	17.8		27.9	48.9	43.2	60.9
Holopediidae	2.5		2.9	2.8	0.7	0.9
Leptodoridae	0.8			10.6	23.0	21.8
Maxillopoda						
Copepoda	20.3	1.9	1.9	7.1		10.0
Malacostraca						
Amphipoda						

TABLE A.1. Continued.

Taxon	ETL	HAL	LSP	PRL	RKL	WTL
Crangonyctidae	0.8		9.6		25.2	20.0
Talitridae	17.8		12.5	1.4	2.9	5.5
Isopoda						
Asellidae	1.7	76.9		60.3		
Decapoda						
Cambaridae	1.7	34.6		0.7	30.2	
Actinopterygii						
Osmeriformes						
Osmeridae	14.4		4.8			
Salmoniformes						
Salmonidae				1.4		
Amphibia						
Caudata						
Plethodontidae		13.5			1.4	3.6
Salamandridae				2.1		0.9
Anura						
Hylidae		1.9				
Undetermined aquatic invertebrates	2.5		3.8	3.5	2.9	0.9
Undetermined egg	5.9		1.0	0.7		
Undetermined terrestrial invertebrates	4.2	3.8	1.9	1.4		3.6
Undetermined vertebrates	0.8		1.0		0.7	
Total identified taxa	60	34	38	41	37	49