

Shifts in the Trophic Ecology of Brook Trout Resulting from Interactions with Yellow Perch: an Intraguild Predator–Prey Interaction

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Abstract.—In size-structured populations, predator–prey interactions may be preceded by a phase of resource competition earlier in ontogeny, with potential consequences for population dynamics and resource management. We hypothesized that brook trout *Salvelinus fontinalis* and yellow perch *Perca flavescens* would compete for shared resources and interact as predator and prey. We used stable isotopes and stomach content analysis to compare the trophic ecology of brook trout in lakes with and without yellow perch. Percent littoral resource use by brook trout differed between perch and nonperch systems, ranging from approximately 50% to 100% in nonperch lakes compared with 10–70% in perch lakes. Nonpiscivorous-sized brook trout (fork length [FL] < 25 cm) showed a significant ontogenetic diet shift toward greater pelagic resource use during growth from 15 to 25 cm in sympatry with yellow perch. Nonpiscivorous-sized brook trout in nonperch lakes consumed a mixture of zoobenthos, zooplankton, and littoral prey fish. In contrast, in lakes containing yellow perch, nonpiscivorous-sized brook trout fed primarily on pelagic prey. Brook trout shifted to piscivory at a FL of approximately 25 cm in both perch and nonperch systems. Isotopic results and stomach content analysis indicated that yellow perch were the primary prey of piscivorous-sized brook trout (FL > 25 cm) in perch lakes, occurring in 66–100% of the brook trout sampled and accounting for over 97% of the diet by weight. Overall, the presence of yellow perch resulted in a shift in the energetic basis for brook trout production from primarily littoral to primarily pelagic. The shift in brook trout food web position was associated with a decline in brook trout catch per unit effort. We conclude that brook trout and yellow perch interact as intraguild predator and prey and that the interaction is dominated by yellow perch.

In size-structured populations, predator–prey interactions may be preceded by a phase of resource competition earlier in ontogeny. Such mixed interactions are referred to as intraguild predation (Polis et al. 1989). The combination of predation and competition that characterizes intraguild predation leads to unique population dynamics not observed in simple unstructured interactions (Polis and Holt 1992; De Roos and Persson 2005). In particular, prey may have both a negative and a positive effect on their predator depending on whether the interaction is dominated by competition or predation (Olson et al. 1995). This scenario may lead to unique outcomes such as the imposition of a recruitment bottleneck on the predator population by prey species and the possible occurrence

of alternative states of either predator or prey dominance due to priority effects (Persson et al. 2007).

Fish populations are size-structured and many species undergo ontogenetic niche shifts during growth from larval to adult stages (Werner and Gilliam 1984). The fact that piscivores typically pass through a succession of diet shifts from small to large prey suggests intraguild predation may be a common interaction among fish species (Polis and Holt 1992). With recent interest in ecosystem-based management of fisheries, the effect of fish community interactions on the population dynamics of exploited fish populations has received particular attention (Evans et al. 1987; Mangel and Levin 2005). Within the suite of community interactions, mixed competition–predation interactions are hypothesized to lead to alternative states in commercial and sport fisheries for top predators due to the potential for prey fish to impose a juvenile recruitment bottleneck on the predator (Walters and Kitchell 2001; Post et al. 2002). Despite extensive theoretical examination of what such mixed interactions may mean for fish population dynamics, few examples of intraguild predation among fish

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species have been studied in the field. Examples are limited to the interaction between rainbow trout *Oncorhynchus mykiss* and reidside shiner *Richardsonius balteatus* (Johannes and Larkin 1961), yellow perch *Perca flavescens* and roach *Rutilus rutilus* (Bystrom et al. 1998), and largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* (Olson et al. 1995).

Brook trout *Salvelinus fontinalis* and yellow perch are two species whose ranges overlap across much of northeastern North America (Scott and Crossman 1973). Both species are generalists, feeding on zooplankton, aquatic insects, and fish. Before attaining piscivorous sizes (approximately 25 cm fork length [FL] for brook trout and 15 cm for yellow perch), brook trout and yellow perch both preferentially exploit zoobenthos in the littoral zone of lakes (Keast 1977; Fraser 1980; Tremblay and Magnan 1991). Yellow perch are also potential prey for piscivorous-sized brook trout. A review of the fisheries management literature on the introduction of yellow perch to brook trout lakes reveals a consistent pattern of decline in brook trout population density and angler catch per unit effort (CPUE) after introduction (Smith 1938; Hayes and Livingstone 1955; Zilliox and Pfeiffer 1956, 1960; Flick and Webster 1992). Furthermore, stocking brook trout into lakes containing yellow perch has met with consistent failure regardless of lake size or fish community composition (Eschmeyer 1938; Fraser 1972; Kerr 2000). The low survival of stocked brook trout is thought to result from resource competition with yellow perch (Fraser 1978). On the other hand, studies of native coexisting populations suggest yellow perch can be a major prey item of brook trout resulting in rapid growth of piscivorous size-classes of brook trout (Baldwin 1948). These observations suggest brook trout and yellow perch may interact as intraguild predator and prey.

We hypothesized that brook trout and yellow perch would compete for shared resources and interact as predator and prey. To test for resource competition between the two species, we compared the carbon isotopic signature and diet of brook trout with FL less than 25 cm (referred to as nonpiscivorous-sized brook trout) in lakes with and without yellow perch. Based on previous studies of the effects of yellow perch on zoobenthos (Post and Cucin 1984), we expected the presence of yellow perch to reduce the availability of zoobenthos to nonpiscivorous-sized brook trout causing them to shift from littoral to pelagic resource use. To test for predation by brook trout with FL greater than 25 cm (referred to as piscivorous-sized brook trout) on yellow perch, we used stomach content analysis and nitrogen isotopic signatures to quantify the

contribution of yellow perch to brook trout diet. We hypothesized that yellow perch would be the dominant prey item of brook trout. Finally, we examined the population level outcome of the brook trout–yellow perch interaction by comparing brook trout abundance in lakes with and without yellow perch. We expected resource competition to dominate the interaction resulting in reduced brook trout abundance in sympatry with yellow perch.

Methods

We examined the interaction between brook trout and yellow perch in three oligotrophic, Laurentian Shield lakes (referred to as perch lakes and coded as P1, P2, and P3). The three sympatric populations were compared with four populations from oligotrophic lakes that do not contain yellow perch (referred to as nonperch lakes and coded as NP1 to NP4). The study lakes are located in Algonquin Provincial Park, Ontario (45°35'N, 78°20'W). The physical characteristics and the complete species composition of the fish communities of the seven lakes are given in Table 1. Yellow perch were native to the three perch lakes. The study lakes were similar in size and water clarity with Welcome Lake having the greatest surface area and Loontail Lake having the shallowest maximum depth. The three perch lakes were selected such that fish community compositions were as similar to each other as possible. Nonperch lakes were selected to establish a baseline for brook trout resource use in a variety of fish community types. Yellow perch was the only species unique to all three perch systems. Other potential competitors such as creek chub, white sucker, pumpkinseed, and brown bullhead occurred in both perch and nonperch lakes. Six of the lakes are open to recreational fishing and accessible by canoe and portage only. Stringer Lake has been closed to fishing since 1994. Brook trout is the only species sought by anglers in all seven lakes.

Fish sampling.—In 2001, lakes were sampled for fish and invertebrates over a period of 3 to 5 d, twice during the open-water season: once between June 1 and July 12 and again between August 15 and September 15. Brook trout and yellow perch were collected live between 0600 and 1000 hours and between 1700 and 2100 hours by means of multi-filament gill nets 46.7 m long by 2 m high and composed of six 7.6-m-long sections with mesh sizes ranging from 25.4 mm to 76.2 mm and increasing in size by increments of 12.7 mm. This range of mesh sizes effectively sampled brook trout with a FL greater than 15 cm and yellow perch with a FL greater than 8 cm. Nets were set on the bottom perpendicular to the shore across a depth gradient of 2–9 m. Two to four nets were set

TABLE 1.—Physical characteristics and fish community composition of the study lakes. Species list is compiled from direct observations and the Ontario Ministry of Natural Resources lake inventory database. Species codes are as follows: BT, brook trout *Salvelinus fontinalis*; RW, round whitefish *Prosopium cylindraceum*; LS, longnose sucker *Catostomus catostomus*; WS, white sucker *C. commersonii*; NRD, northern redbelly dace *Phoxinus eos*; FSD, finescale dace *P. neogaeus*; LC, lake chub *Couesius plumbeus*; GS, golden shiner *Notemigonus crysoleucas*; CS, common shiner *Luxilus cornutus*; BNS, blacknose shiner *Notropis heterolepis*; BNM, bluntnose minnow *Pimephales notatus*; FM, fathead minnow *P. Promelas*; CC, creek chub *Semotilus atromaculatus*; FF, fallfish *S. corporalis*; PD, pearl dace *Margarisus margarita*; BB, brown bullhead *Ameiurus nebulosus*; BS, brook stickleback *Culaea inconstans*; TP, trout-perch *Percopsis omiscomaycus*; PS, pumpkinseed *Lepomis gibbosus*; YP, yellow perch *Perca flavescens*; ID, Iowa darter *Etheostoma exile*; and MS, mottled sculpin *Cottus bairdii*.

Lake	Lake code	Surface area (ha)	Maximum depth (m)	Mean depth (m)	Secchi disk depth (m)	Fish community composition
Nonperch lakes						
Scott	NP1	28	25.0	7.3 ^a	7.5	BT, NRD, FM, BS
Gull	NP2	26	16.0		5.9	BT, LS, NRD, GS, CS, BNS, BNM, BB, PS, ID
Stringer	NP3	34	21.0	6.5	9.0	BT, WS, NRD, FSD, BNM, CC, PD, BS, PS
Welcome	NP4	260	22.9	9.4	5.2	BT, LS, WS, NRD, FSD, LC, FM, CC, BS
Perch lakes						
Nepawin	P1	35	17.0	5.8	5.8	BT, WS, NRD, GS, CS, BNS, CC, PD, BB, YP, MS
Queer	P2	77	13.4	3.2	4.4	BT, RW, WS, NRD, GS, BNS, FF, PD, BB, PS, YP
Loontail	P3	99	9.5	4.5	4.0	BT, WS, CS, BNS, BNM, CC, FF, PD, BB, TP, PS, YP

^a Not determined.

simultaneously and checked every 30 min. Nets were set in areas of highest brook trout density based on information from the Algonquin Fisheries Assessment Unit, local anglers, and angling surveys of the lakes. Catch per unit effort was calculated as the mean number of brook trout (FL > 15 cm) per 30-min net set.

Captured live trout were held in a tank containing aerated cold water (10–15°C) for a maximum of 1 h before processing. In cases where brook trout were highly stressed from gillnetting or where sufficient brook trout had been sampled in the size-class, brook trout were returned immediately to the lake. These brook trout are counted in the CPUE data but stomach contents and tissue samples were not taken. The total number of brook trout sampled in each lake was as follows: NP1 = 37, NP2 = 32, NP3 = 20, NP4 = 57, P1 = 37, P2 = 36, P3 = 26. Brook trout were anesthetized by immersion in a 60-mg/L clove oil bath (Anderson et al. 1997). Fork length was recorded and the adipose fin was clipped. Brook trout stomachs were flushed with water and the stomach contents were preserved in 5% formaldehyde solution for subsequent analysis. A 20-mg muscle biopsy was taken from the dorsal white muscle using a biopsy needle and preserved on ice in the field. Muscle tissue samples were later frozen and then freeze-dried in preparation for stable isotope analysis. Brook trout were allowed to recover in a tank of cold water for 30 min before being released back to the lake. Stable isotope analyses were performed on a subsample of the total number of brook trout sampled in each lake. Yellow perch were sacrificed, preserved on ice in the field, and later frozen. A 0.5-g sample of yellow perch dorsal white muscle tissue was taken in

the laboratory and freeze-dried in preparation for stable isotope analysis.

Stomach content analysis.—Sampling of brook trout during peak foraging times (dusk and dawn) resulted in stomach contents consisting of predominantly whole undigested prey items, with the exception of fish, which were sometimes partially digested. Fifteen brook trout, ranging in size from 15 to 40 cm, were sacrificed following stomach flushing of zooplankton, zoobenthos, or fish prey and their stomachs examined to determine the effectiveness of the stomach pumping technique. No prey items remained in the stomachs. Thus, samples are considered to be the entire stomach contents for each brook trout. Less than 5% of brook trout had empty stomachs and were excluded from the stomach content analysis. Prey items were identified to genus for zooplankton, order or family for insects, and genus or species for fish. Prey items of the same type from each stomach were pooled, dried at 60°C, and weighed to the nearest 0.1 mg.

Diet composition is expressed in terms of percent occurrence and percent weight. Percent occurrence is the percentage of brook trout sampled that had consumed the prey item. Percent weight is the total dry weight of each prey item expressed as a percentage of the overall weight of the stomach contents of all brook trout in the sample. Stomach content analysis was used to indicate the foraging behaviour of brook trout. Prey were classified as either plankton, benthos, or fish. Dipteran pupae were classified as plankton as brook trout forage on dipteran pupae in the water column together with zooplankton and *Chaoborus*.

Invertebrate sampling.—Zoobenthos and zooplankton were used to establish the baseline isotopic

TABLE 2.—Pelagic and littoral $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ baselines for the seven study lakes (means \pm SEs); $n = 4$ for pelagic baselines and $n = 3$ for littoral baselines.

Lake	Pelagic		Littoral	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
NP1	2.66 ± 0.28	-31.98 ± 0.56	5.07 ± 0.33	-24.05 ± 0.60
NP2	2.99 ± 0.32	-32.15 ± 0.51	3.94 ± 0.25	-25.04 ± 0.17
NP3	3.04 ± 0.14	-30.77 ± 0.35	4.03 ± 0.23	-25.35 ± 0.84
NP4	2.59 ± 0.17	-31.64 ± 0.32	3.88 ± 0.40	-24.20 ± 0.32
P1	3.19 ± 0.11	-31.41 ± 0.61	3.23 ± 0.60	-24.83 ± 0.87
P2	3.37 ± 0.14	-30.60 ± 0.21	3.66 ± 0.31	-25.29 ± 0.76
P3	4.08 ± 0.10	-32.06 ± 0.13	2.87 ± 0.46	-24.04 ± 1.18

signature of littoral benthic (hereafter referred to as littoral) and pelagic resources, respectively. The profundal zone of lakes is a third isotopic endpoint that differs from pelagic and littoral endpoints. We did not include a profundal endpoint in our analysis as profundal *Chironomus* species were not found in the stomachs of brook trout and neither brook trout nor yellow perch are known to feed on prey in the anoxic profundal zone of lakes. Fish may also obtain carbon and nitrogen by feeding on prey of terrestrial origin; however, in lake environments, brook trout and yellow perch consume primarily aquatic prey (Keast 1977; Magnan 1988). Terrestrial prey were a minor component of brook trout diet in the present study.

Invertebrate samples were collected twice over the open-water season at the same time as fish sampling occurred. Benthic invertebrate samples were collected using a kick net and an Ekman grab sampler. Samples were sorted in the field, frozen, and subsequently freeze-dried in preparation for stable isotope analysis. The littoral baseline for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was defined as the mean ($n = 3$) of the average signatures for Amphipoda, Ephemeroptera (*Hexagenia* spp.), and littoral chironomid larvae. These three taxa were chosen because they were known to commonly occur in brook trout stomachs. Benthic invertebrates of the same type were pooled such that individual samples included homogenized tissue from three to six individuals. Two to six samples were analyzed for each of the three types of benthic invertebrates used to establish the baseline. Pelagic zooplankton, primarily *Daphnia* and *Holopedium* spp., were used to define the pelagic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline. *Daphnia* and *Holopedium* are herbivorous zooplankton commonly consumed by fish. Zooplankton were collected in June and August using a 220- μm -mesh plankton net towed horizontally at a depth of 1–3 m. Bulk zooplankton samples were collected from two tows in both June and August and preserved frozen. In the laboratory, Cladocera (primarily *Daphnia* and *Holopedium* spp.)

were separated from the bulk sample and subsequently freeze-dried before stable isotope analysis. June and August samples ($n = 2$ in each month) were analyzed separately and the average stable isotopic signature of the four samples was used as the pelagic carbon and nitrogen baseline. The littoral and pelagic baselines for the seven study lakes are presented in Table 2.

The isotopic signature of zooplankton and zoobenthos can vary seasonally (Grey et al. 2004; Perga and Gerdeaux 2006). As a result, estimates of carbon and nitrogen isotopic baselines could be biased if samples were collected at different times of the year in different lakes. Sampling of isotopic baselines at a similar time of year in all study lakes reduced any differences between lakes in baseline estimates that might result from seasonal fluctuations in the isotopic signatures of baseline organisms. Within season fluctuations in isotopic baselines are not reflected in fish muscle tissue since muscle tissue integrates prey isotopic signals over the entire open water season (Perga and Gerdeaux 2005). As a result, fish muscle tissue reflects the average baseline signal during the period of fish growth. Thus, isotopic baselines should estimate prey signatures over the warmwater season during which the majority of fish growth occurs. Littoral and pelagic baselines used in this study incorporate seasonal variation into the estimate of baseline isotopic signatures by averaging the signatures of samples collected in June and August.

Stable carbon and nitrogen isotope analyses were performed using a continuous flow Finnigan MAT Delta plus mass spectrometer at the G. G. Hatch Isotope Laboratory at the University of Ottawa. The percent carbon and nitrogen of tissue samples was analyzed simultaneously on an Elementar Vario EL III elemental analyser connected to the mass spectrometer via a ConFlo II. Stable isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material, and determined as

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000,$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Analytical precision was 0.2‰ for carbon and nitrogen. Within-sample variation was estimated from analysis of 23 duplicate tissue samples. The relative standard deviation (SD) was 0.4% for $\delta^{13}\text{C}$ and 1.3% for $\delta^{15}\text{N}$.

To compare carbon and nitrogen isotopic signatures between fish populations, it is necessary to account for differences in the carbon and nitrogen isotopic baselines of the study lakes. We expressed carbon isotopic signatures in terms of percent littoral resource

use and nitrogen isotopic signatures as baseline corrected trophic position. The relative contribution of littoral versus pelagic carbon to brook trout and yellow perch diet was estimated by means of a two-source mixing model with the lake-specific end members presented in Table 2 (Vander Zanden et al. 2003). Percent littoral resource use was calculated as

$$100 \times (\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic}}).$$

Brook trout and yellow perch trophic position was estimated with the formula

$$\text{trophic position}_{\text{fish}} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4] + 2,$$

where 3.4 is the assumed per trophic level increase in $\delta^{15}\text{N}$ and $\delta^{15}\text{N}_{\text{baseline}}$ is determined for each fish by calculating a weighted average of lake-specific pelagic and benthic $\delta^{15}\text{N}$ endpoints based on the percent contribution of each food source as determined by $\delta^{13}\text{C}$ (Deniro and Epstein 1981; Vander Zanden and Rasmussen 1999).

Tissue lipid content may influence $\delta^{13}\text{C}$ signatures as lipid is depleted by approximately 6.5‰ relative to protein (Pinnegar and Polunin 1999; Sweeting et al. 2006). We used the C:N ratio of muscle tissue as a proxy for lipid content (Sweeting et al. 2006). We tested for differences in C:N between populations and for significant correlations between C:N and $\delta^{13}\text{C}$ within populations to test for an effect of lipid content on $\delta^{13}\text{C}$. The C:N ratio of muscle tissue from the lake NP1 population was significantly higher than all other populations with the exception of lake NP4 (analysis of variance [ANOVA]: $F_{6, 187} = 7.46$, $P < 0.0001$, followed by Tukey's honestly significant difference [HSD] test). Mean C:N ranged from 3.18 to 3.56 across all seven populations giving a maximum difference in the means of 0.38 units corresponding to a difference in lipid content of approximately 7.9% or a difference in $\delta^{13}\text{C}$ of approximately 0.55‰ (McConnaughey and Mcroy 1979; Sweeting et al. 2006). Populations from nonperch lakes had the highest C:N indicating they had the highest lipid content. As a result, the carbon isotope results for brook trout from nonperch lakes may be biased toward lighter, more pelagic carbon signatures due to the higher lipid content of these populations. Thus, carbon isotope results may underestimate the difference in percent littoral resource use between perch and nonperch lakes. Within populations, there were no significant correlations between C:N and $\delta^{13}\text{C}$ (Pearson correlations ranged in significance from $P = 0.162$ to $P = 0.995$) indicating within population variation in $\delta^{13}\text{C}$ was due to factors other than lipid content.

Results

Patterns in Littoral versus Pelagic Resource Use

The carbon isotopic signature of brook trout muscle tissue revealed marked differences in resource use between systems (Figure 1). In nonperch systems, brook trout growth was predominantly linked to littoral primary production (Figure 1A, B; mean percent littoral = 61.4, 61.7, 84.2, and 81.7% for populations in lakes NP1, NP2, NP3, and NP4, respectively). There were significant differences among nonperch systems in the ontogenetic pattern of brook trout resource use. Lake NP1 and NP2 populations were characterized by a decline in percent littoral resource use with increasing brook trout length ($r^2 = 0.29$ and 0.30 ; $F = 13.30$ and 7.42 ; $P = 0.001$ and 0.014 ; $n = 34$ and 19 for lakes NP1 and NP2, respectively). The relationship between percent littoral resource use and brook trout length was not significantly different between lakes NP1 and NP2 (Figure 1A; analysis of covariance [ANCOVA] lake \times length: $F_{1, 53} = 0.993$, $P = 0.324$; lake: $F_{1, 53} = 0.949$, $P = 0.335$). In contrast, the lake NP3 and NP4 populations showed no change in percent littoral resource use with brook trout length ($r^2 = 0.129$ and 0.0002 ; $F = 2.51$ and 0.003 ; $P = 0.131$ and 0.954 ; $n = 19$ and 24 for lakes NP3 and NP4, respectively) and mean percent littoral resource use did not differ between the two populations (Figure 1B; t -test: $t = 0.650$, $df = 41$, $P = 0.519$, pooled mean 82.8%).

In lakes containing yellow perch, brook trout production was predominantly linked to pelagic primary production (Figure 1C). The ontogenetic pattern in brook trout resource use was best described by a positive quadratic function with a minimum value at approximately 28 cm indicating a shift toward greater reliance on pelagic prey during growth from 15 to 28 cm (Figure 1C; $r^2 = 0.41$, 0.54 , and 0.32 ; $F = 13.34$, 13.96 , and 5.64 ; $P < 0.001$; $n = 41$, 27 , and 27 for lake P1, P2, and P3 populations, respectively). A second-order function explained a significantly greater portion of the variance than a first-order function in all three perch systems ($F = 24.8$, 27.9 , and 11.3 ; $P < 0.01$ for lakes P1, P2, and P3, respectively). The relationship between percent littoral resource use and brook trout length did not differ among the three perch lakes (Figure 1C; ANCOVA lake: $F_{2, 95} = 1.715$, $P = 0.186$; lake \times length \times length²: $F_{3, 95} = 0.670$, $P = 0.573$). Mean percent littoral resource use of non-piscivorous-sized brook trout was lower in yellow perch systems (48.7% versus 77.5%; t -test: $t = 4.75$, $df = 5$, $P = 0.005$, where the 20–25-cm size-class is excluded from the analysis for perch systems). The general pattern in brook trout diet across all three perch lakes was a shift from approximately 50% littoral

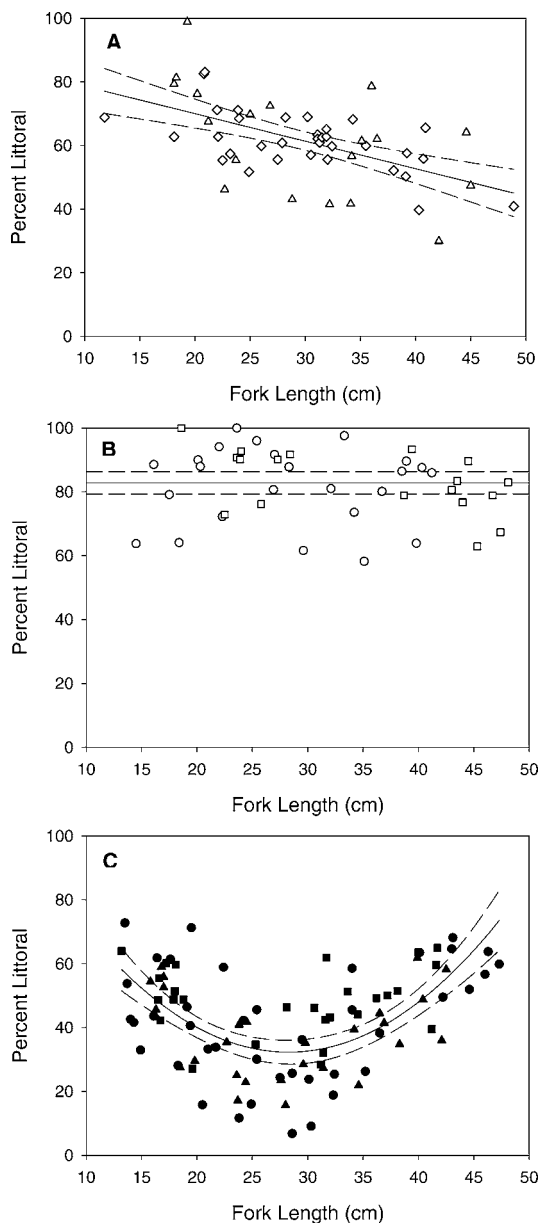


FIGURE 1.—Ontogenetic pattern of littoral versus pelagic resource use by brook trout based on muscle tissue $\delta^{13}\text{C}$. Solid lines are the best-fit regression or the mean; dashed lines are the 95% confidence intervals. Panel (A) shows the results for lakes NP1 (diamonds) and NP2 (open triangles) ($y = 87.3 - 0.865x$; $r^2 = 0.31$, $P < 0.001$, $n = 53$), panel (B) the results for lakes NP3 (open squares) and NP4 (open circles) (mean = 82.8, $n = 43$), and panel (C) the results for lakes P1 (filled circles), P2 (filled triangles), and P3 (filled squares) ($y = 123.46 - 6.447x + 0.114x^2$; $r^2 = 0.38$, $P < 0.001$, $n = 95$).

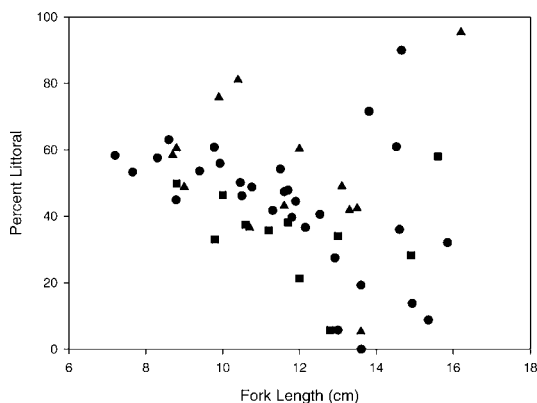


FIGURE 2.—Ontogenetic pattern of littoral versus pelagic resource use by yellow perch from the three perch lakes. Symbols represent lakes P1 (circles), P2 (triangles), and P3 (squares).

resource use at small size-classes (FL < 20 cm) to 25% at intermediate sizes (FL = 25–30 cm) followed by a second shift to approximately 60% littoral resource use at large sizes (FL > 35 cm).

Yellow perch diet was also characterized by a shift in littoral versus pelagic resource use with size (Figure 2). Small size-classes of yellow perch (FL = 7–10 cm) relied on a mixture of littoral and pelagic prey with carbon isotopic signatures indicating approximately 40–60% reliance on littoral resources. Variation in percent littoral resource use increased over the 10–14-cm size interval due to the occurrence of yellow perch with a greater reliance on pelagic resources in this size range. Minimum percent littoral resource use occurred in the 13–14-cm size range in all three study systems; however, littoral resource use continued to range up to 60%. Resource use of yellow perch greater than 13 cm FL was characterized by a high degree of variability. Individual yellow perch ranged from 9% to 95% littoral resource use in the 14–16-cm size range. Overall, yellow perch in lake P1 showed a significant decline in percent littoral resource use with size ($r^2 = 0.17$, $F = 5.76$, $P = 0.023$, $n = 29$); however, yellow perch from lakes P2 and P3 showed no significant trend with size ($r^2 = 0.002$ and 0.011 , $F = 0.02$ and 0.1 , $P = 0.89$ and 0.76 , $n = 12$ and 10 for lakes P2 and P3, respectively).

Diet Analysis

Stomach content analysis revealed differences in the feeding habitats of nonpiscivorous-sized brook trout in perch versus nonperch systems. Diet data indicated the dominance of planktonic feeding by nonpiscivorous-sized brook trout from perch systems. Cladocera, dipteran pupae, and yellow perch larvae were the dominant prey items indicative of planktonic feeding

TABLE 3.—Diet composition of nonpiscivorous-sized brook trout (FL < 25 cm). Values are the mean percent occurrence and percent dry weight, with ranges in parentheses. The number of stomachs examined was 71 in nonperch lakes and 53 in perch lakes. The category "Other" includes terrestrial insects and infrequently consumed aquatic invertebrates such as leeches.

Prey item	Nonperch lakes		Perch lakes	
	Occurrence	Weight	Occurrence	Weight
Plankton				
<i>Chaoborus</i>	34.0 (0–81)	1.3 (0–4)	20.6 (0–43)	2.3 (0–4)
Cladocera	46.2 (17–78)	19.1 (0–50)	31.2 (29–36)	25.3 (0.1–66)
Dipteran pupae	35.8 (18–69)	1.4 (0–5)	59.3 (45–81)	10.6 (0–22)
Total	61.2 (17–97)	21.8 (0–54)	70.6 (54–86)	38.2 (1–80)
Benthos				
Chironomid larvae	27.3 (9–39)	0.2 (0–0.3)	45.1 (14–64)	1.2 (0.1–3)
Ephemeroptera	53.4 (17–83)	15.5 (2–29)	4.8 (0–14)	0.8 (0–2)
Trichoptera	20.0 (6–31)	1.8 (0–6)	9.3 (0–19)	<0.1 (0–0.1)
Odonata	20.9 (0–36)	2.3 (0–6)	1.6 (0–5)	1.3 (0–4)
Amphipoda	4.8 (0–19)	2.4 (0–10)	0.0	0.0
Total	71.2 (39–83)	22.2 (2–36)	49.8 (19–67)	3.3 (0.2–9)
Fish				
Larval perch	^a	^a	47.7 (0–100)	53.0 (0–95)
Other fish	51.3 (25–67)	51.3 (19–81)	0	0
Other	6.2 (0–14)	4.7 (0–12)	13.6 (0–36)	5.5 (0–8)

^a Not applicable.

(Table 3). Dipteran pupae were considered a planktonic prey item as brook trout forage on pupae in the water column. However, dipteran pupae have a littoral isotopic signature and would not contribute to the observed isotopic shift to pelagic signatures in nonpiscivorous-sized brook trout from perch lakes. The occurrence of yellow perch larvae in the diet of nonpiscivorous-sized brook trout was limited to samples collected between June 19 and July 7. Chironomid larvae were the only prey indicative of benthic feeding that commonly occurred in the diet of brook trout from perch systems. In contrast, brook trout from nonperch systems consumed a mixture of benthos, plankton, and fish. In particular, the occurrence of Ephemeroptera was significantly higher in nonperch versus perch systems (Student's *t*-test: *t* = 2.876, *df* = 5, *P* = 0.035). Fish consumed in nonperch systems included northern redbelly dace, fathead minnow, and brook stickleback.

Stomach content data indicated a transition to piscivory at approximately 25 cm FL in brook trout from both nonperch and perch lakes (Figure 3). Piscivory in the 15–25-cm size-class was more common in brook trout from nonperch lakes. Consumed prey fish had a mean length of 2.9 cm and a maximum length of 5.0 cm in nonperch systems versus a mean of 7.6 cm and a maximum of 11.6 cm in perch systems. Yellow perch was the dominant prey item of piscivorous-sized brook trout in perch systems in terms of both percent occurrence and percent dry weight (Table 4). Mean trophic position of large piscivorous brook trout (FL ≥ 40 cm) ranged from 4.18 to 4.36 in perch systems. The difference in trophic position

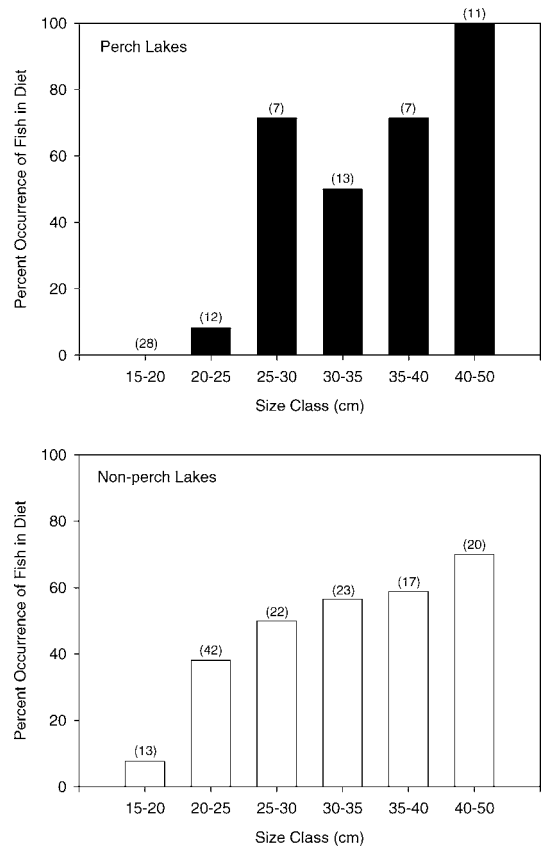


FIGURE 3.—Frequency of occurrence of fish in the diet of brook trout by size-class for perch and nonperch lakes. Sample sizes are indicated in parentheses above the individual bars. Larval fish (FL < 35 mm) were excluded from the data set.

TABLE 4.—Brook trout piscivory in perch lakes. The percent occurrence and percent dry weight of fish in the diet of piscivorous brook trout (fork length > 25 cm). The comparisons of trophic position and percent littoral resource use are for large brook trout (FL > 40 cm) and their prey, yellow perch (FL = 6–12 cm).

Lake	Fish consumption ^a		% Perch in diet	Trophic position ^b		Littoral use	
	Occurrence	Weight		Trout	Perch	Trout	Perch
P1	93	99	100	4.23 (0.07)	3.54 (0.11)	59.8 (6.5)	51.8 (6.6)
P2	66.7	97	100	4.18 (0.13)	3.43 (0.22)	51.2 (11.5)	57.0 (14.5)
P3	100	92	100	4.36 (0.05)	3.57 (0.11)	56.9 (11.8)	37.4 (9.3)

^a Number of stomachs examined was 10, 15, and 15 in lakes P1, P2, and P3, respectively.

^b Sample sizes for isotope data are as follows: P1: $n = 8$ and 17; P2: $n = 4$ and 8; and P3: $n = 4$ and 6; for brook trout and yellow perch, respectively.

between brook trout and yellow perch provides an estimate of perch contribution to trout diet and ranged from 0.69 to 0.79 indicating that, on average, 74% of the energy for piscivorous brook trout growth was derived from yellow perch. In lakes P1 and P2, the percent littoral resource use of brook trout greater than 40 cm FL converged on that of their prey, yellow perch; however, this was not the case in the lake P3 population where perch relied on a greater proportion of pelagic resources (Table 4). Consistent with a transition to piscivory at 25 cm FL, brook trout trophic position increased with brook trout length over the 25–50-cm size range in all three perch lakes (Figure 4; $r^2 = 0.84, 0.71$, and 0.34 ; $P < 0.001, <0.001$, and 0.014 ; $n = 22, 14$, and 17 for lakes P1, P2, and P3, respectively); however, there was no significant relationship between brook trout length and trophic position in the 15–25-cm size range (Figure 4; $r^2 = 0.13$ and 0.01 ; $P = 0.206$ and 0.746 ; $n = 13$ and 12 for lakes P1 and P2, respectively; analysis omitted for lake P3 due to insufficient size range).

Brook Trout Abundance

Brook trout CPUE was four times higher in nonperch versus perch lakes suggesting decreased brook trout density in sympatry with yellow perch (Table 5; t -test: $t = 3.260$, $df = 5$, $P = 0.023$).

Discussion

Competition between Brook Trout and Yellow Perch

Dietary and isotopic results supported our hypothesis of resource competition between yellow perch and nonpiscivorous-sized brook trout. In the presence of yellow perch, nonpiscivorous-sized brook trout relied on a lower proportion of littoral resources for growth than did brook trout from nonperch lakes. Furthermore, nonpiscivorous-sized brook trout showed a consistent pattern of decreasing littoral resource use during growth from 15 to 25 cm in length in perch lakes, a pattern not observed in nonperch lakes. Consistent with these observations, nonpiscivorous-sized brook trout diet data indicated a significantly lower occurrence of

large zoobenthos, such as Ephemeroptera larvae, in the presence of yellow perch. These results indicate a niche shift in brook trout in the presence of yellow perch and suggest the two species compete for shared resources.

Based on the feeding ecology of brook trout and yellow perch, we expected evidence for resource competition between the two species to be strongest for nonpiscivorous-sized brook trout in the 15–25-cm size-class. Brook trout and yellow perch have been shown to pass through a similar pattern of ontogenetic diet shifts, which suggests the possibility for significant dietary overlap and competition for shared resources. Young-of-year (age 0) brook trout feed in the littoral zone on a mixture of zoobenthos and zooplankton (Curry et al. 1993; Venne and Magnan 1995), while age-0 yellow perch are zooplanktivorous and feed primarily in the pelagic zone (Arts and Sprules 1989). Brook trout of age 1 and older (generally FL > 8 cm) feed on a wide variety of prey items (Ricker 1932a); however, zoobenthos is the dominant prey in the absence of strong resource competition (Fraser 1980; Fraser and Loftus 1983; Tremblay and Magnan 1991; Lacasse and Magnan 1992). Similarly, at a FL of approximately 10 cm, yellow perch become primarily benthivorous (Keast 1977; Hjelm et al. 2000). Brook trout longer than 25 cm become piscivorous if suitable prey are available (East and Magnan 1991; Morinville and Rasmussen 2006) and fish may become the primary prey item accounting for 60–90% of the diet (Ricker 1932b; Speirs 1974; Flick 1977). Yellow perch shift to piscivory at a length of 15–20 cm (Keast 1977; Hjelm et al. 2000). Thus, the potential for dietary overlap between the two species is particularly strong in the zoobenthivorous niche before the shift to piscivory occurs (10–25 cm for brook trout and 10–15 cm for yellow perch). Our results are consistent with this hypothesis and suggest yellow perch reduce the availability of large zoobenthos causing nonpiscivorous-sized brook trout to exploit small zoobenthos and planktonic prey. This observation is similar to that reported for the interaction between brook trout and

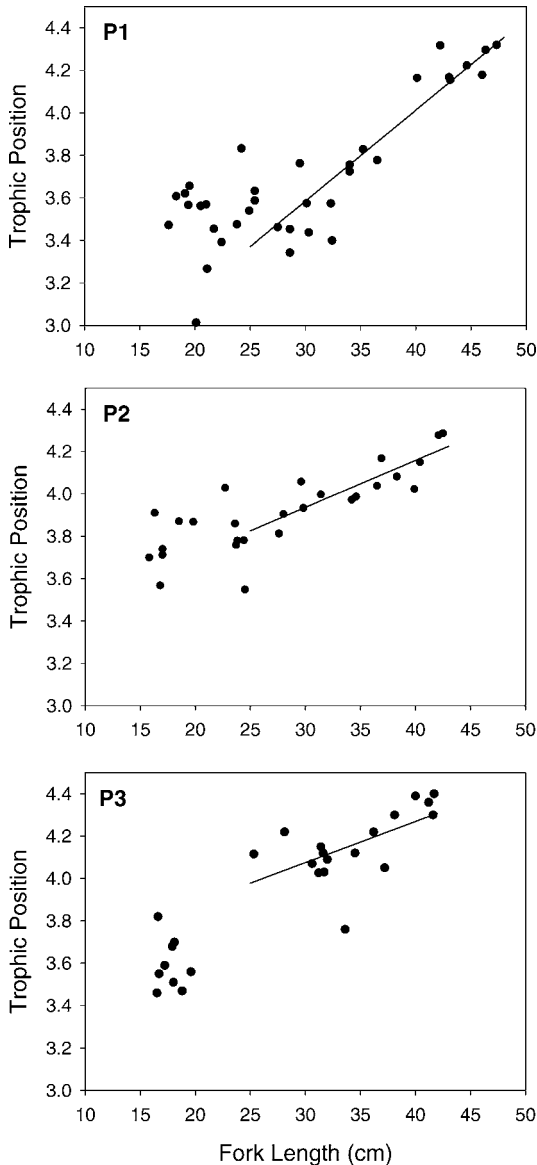


FIGURE 4.—Change in brook trout trophic position with length in the three perch lakes (P1–P3). Solid lines indicate the trend in trophic position in the piscivorous size-class (FL > 25 cm; P1: $y = 2.301 + 0.0428x$; P2: $y = 3.274 + 0.0221x$; P3: $y = 3.493 + 0.0194x$)

white sucker in which white suckers reduce the availability of zoobenthos causing brook trout to shift from a diet dominated by Ephemeroptera to one dominated by *Chaoborus* (Magnan 1988; Tremblay and Magnan 1991). However, in our study systems, it was only in the presence of both white suckers and yellow perch that brook trout exhibited a shift to pelagic resource use.

TABLE 5.—Sampling dates and catch per unit effort (CPUE) of brook trout with fork lengths greater than 15 cm in perch and nonperch sample lakes. Effort is the total number of 30-min net sets over the two sample dates.

Lake	Sample dates	Effort	Catch (<i>n</i>)	CPUE
Nonperch lakes				
NP1	Jun 23–24, Aug 19–20	38	40	1.05
NP2	Jul 9–12, Aug 27–29	18	36	2.00
NP3	Jun 6–9, Aug 25–26	23	30	1.30
NP4	Jun 14–16, Aug 22–24	65	57	0.88
Mean				1.31
Perch lakes				
P1	Jun 2–4, Aug 16–19	82	24	0.29
P2	Jul 5–7, Sep 4–7	113	34	0.30
P3	Jun 19–21, Sep 9–12	58	26	0.45
Mean				0.35

The observation of a decline in littoral resource use by brook trout in the presence of yellow perch is consistent with previous research showing yellow perch reduce the abundance of benthic invertebrates in lakes and alter the size distribution of prey (Post and Cucin 1984; Diehl 1992). Reduced abundance or mean size, or both, of littoral zoobenthos leads to stunted growth in yellow perch populations and may alter the pattern of ontogenetic diet shifts resulting in a greater reliance on zooplankton prey (Persson 1987; Heath and Roff 1996; Iles and Rasmussen 2005). Stable isotope analysis indicated a range of 40–95% contribution of pelagic carbon to yellow perch diet in the 10–14-cm size range in all three yellow perch populations suggesting limited consumption of zoobenthos during growth through this size interval. Furthermore, although we did not examine yellow perch growth for this study, an examination of yellow perch growth in lake NP1 found yellow perch to be stunted in the 10–14-cm size-class (growth through this size interval spanned 4–5 years). Overall, yellow perch resource use in all three study lakes and the observation of stunted growth in the lake NP1 yellow perch population was consistent with an environment of limited zoobenthos availability in perch lakes.

Resource competition is only one of several possible explanations for an observed niche shift. Diet shifts may also result from behavioral interactions such as predator avoidance (Diehl and Eklov 1995; Schmitz 1998), or the introduction of new optimal prey, such as planktivorous prey fish (Martin 1970). It is unlikely that predator avoidance behavior led to the observed niche shift in brook trout. The maximum size of yellow perch recorded in the three perch lakes was 23 cm, a size too small to pose a predation risk to brook trout in the 15–25-cm size-class. On the other hand, the presence of larval yellow perch does present a novel pelagic prey item to brook trout. Yellow perch larvae

(FL < 30 mm) consume zooplankton and as a result have a pelagic $\delta^{13}\text{C}$ signature and a $\delta^{15}\text{N}$ signature heavier than that of zooplankton (Keast 1977; Murchie and Power 2004). If larval perch were readily available and energetically optimal, nonpiscivorous-sized brook trout may shift to feeding on larval perch regardless of whether the presence of yellow perch altered zoobenthos availability. Nonpiscivorous-sized brook trout did consume larval yellow perch (the size range found in stomachs was 12–37 mm); however, the observed shift to pelagic carbon isotopic signatures by nonpiscivorous-sized brook trout during growth from 15 to 25 cm was not associated with any corresponding increase in trophic position. This result suggests larval perch made a limited contribution to brook trout diet. This may be because larval perch growth is rapid and perch grow through the vulnerable 15–30-mm size-class in approximately 20 d; therefore, larval perch may only be available to nonpiscivorous-sized brook trout during a limited period (Cucin and Faber 1985; Power and van den Heuvel 1999). Thus, while yellow perch larvae appear to be an important component of nonpiscivorous-sized brook trout diet based on stomach content analysis, isotopic results suggest they make a limited contribution to the average diet, possibly due the short window of availability. Predation on larval perch likely adds to a diet already dominated by pelagic prey and contributes to the observed shift to pelagic energetic pathways.

The observation of reduced brook trout abundance in perch lakes and similar observations by previous studies (Fraser 1978; Flick and Webster 1992) suggest recruitment to larger size-classes is reduced in the presence of yellow perch. Resource competition during juvenile growth may result in decreased growth and increased mortality if the associated change in resource availability causes significant increases in the energetic costs of foraging. Due to low brook trout densities and consequently small sample sizes per age-class in perch lakes, we were unable to test for differences in growth between nonperch and perch systems. Size-related diet shifts from small to large prey are commonly observed in species of *Salvelinus* and gaps in the size spectrum have been linked to reductions in growth and yield (Forseth et al. 1994; Jansen et al. 2002; Pazzia et al. 2002; Sherwood et al. 2002). Studies of the size-scaling of feeding in Arctic char *S. alpinus*, a species morphologically similar to brook trout, found that foraging efficiency on zooplankton declined in the 12–18-cm size range (Jansen et al. 2003; Bystrom and Andersson 2005). Brook trout probably exhibit a similar size-dependent decline in foraging rate on zooplankton and increased preference for larger prey items. The observed shift to pelagic resource use in the

20–25-cm size-class may come at an energetic cost to nonpiscivorous-sized brook trout with consequences for survival and recruitment to larger size-classes and reduced yield in brook trout sport fisheries (sensu Larkin and Smith 1954); however, further research is needed to test this hypothesis.

A second mechanism that could lead to reduced brook trout abundance in perch lakes is yellow perch predation on age-0 brook trout. Given that previous studies found reduced brook trout recruitment to large size-classes in both native populations and populations stocked as 1-year-old juveniles (Fraser 1978; Flick and Webster 1992), it appears that predation, if any, is not the primary factor explaining reduced recruitment. A study of yellow perch diet in lake NP1 found no evidence for yellow perch predation on age-0 brook trout in late May and early June (Ng 2005); however, further research is necessary to determine whether yellow perch prey on age-0 brook trout.

Brook Trout Predation on Yellow Perch

Our results confirmed the hypothesis that yellow perch would be the primary prey of piscivorous brook trout in perch lakes. In the presence of yellow perch, brook trout with FL greater than 25 cm were highly piscivorous, consuming perch throughout the entire period of lake stratification from June to September. Fish were the single most important prey item with all other prey contributing only marginally to brook trout diet. Piscivorous-sized brook trout preyed exclusively on yellow perch despite the presence of other prey fishes such as various cyprinid species and pumpkinseed. Isotopic results indicated piscivory was associated with increasing trophic position and heavier (more littoral) $\delta^{13}\text{C}$ signatures consistent with intensive feeding on 7–10-cm yellow perch, the size-class of perch consumed by brook trout in our study lakes. Brook trout shifted to piscivory during growth from 25 to 30 cm FL in both nonperch and perch systems. This result is consistent with previous studies and suggests a transition to piscivory at a length of approximately 25 cm is a general characteristic of brook trout populations in both freshwater and marine environments (East and Magnan 1991; Morinville and Rasmussen 2006).

Previous research has shown that variation in juvenile piscivore growth rate alters the timing of the shift to piscivory and may affect piscivore population size structure and density (Olson 1996; Mittelbach and Persson 1998). Piscivory results in increased growth rate, improved condition, and lower overwinter mortality in salmonids (Jonsson 1999; Niva 1999). For brook trout in perch systems, faster juvenile growth would result in an earlier shift to piscivory and the release from competition with yellow perch. Brook

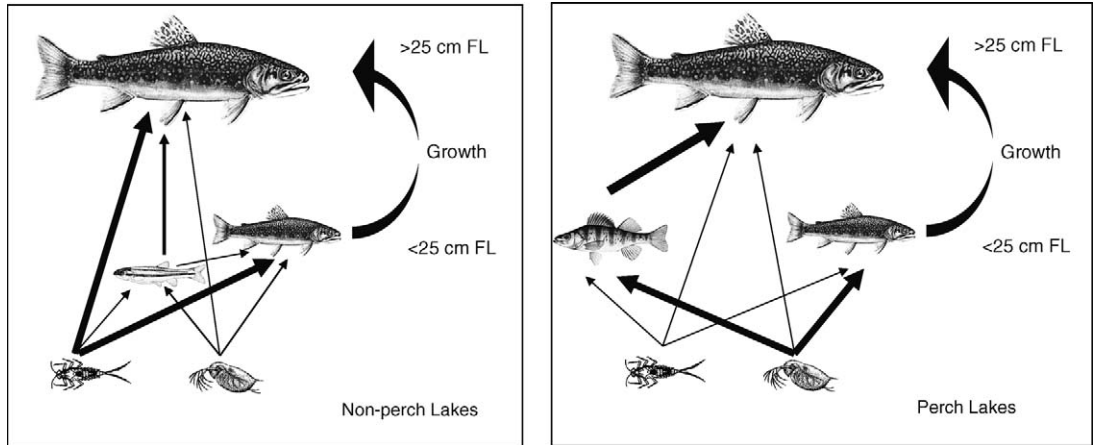


FIGURE 5.—Schematic diagrams of the brook trout food webs in nonperch and perch lakes. Arrow widths represent the proportions of energy derived from each resource. Prey fish in nonperch lakes are represented by a cyprinid. The basal resources are zoobenthos, represented by an Ephemeropteran larva, and zooplankton, represented by *Daphnia*.

trout length at age 2 in May (beginning of third summer) is highly variable, ranging from 17 to 32 cm in Algonquin Park lakes (AFAU 1998), and spanning the size-class for the shift to piscivory. Thus, length at age 2 may be a critical variable in determining the degree of brook trout piscivory before the third winter with subsequent effects on survival and recruitment to larger size-classes. If the niche shift observed for nonpiscivorous-sized brook trout in our study systems comes at an energetic cost, as discussed previously, brook trout may experience reduced growth rates during the first 2 years of life and a later shift to piscivory with potential consequences for survival and recruitment to piscivorous size-classes. The timing of the shift to piscivory is also determined by the size of available prey fish because piscivores must attain sufficient gape size to successfully capture and consume potential prey (Mittelbach and Persson 1998). We found some evidence for a greater rate of piscivory in the 15–25-cm size-class in brook trout from nonperch lakes. The mean size of fish consumed by brook trout in nonperch lakes was smaller than in perch lakes suggesting the observed difference in the frequency of piscivory may reflect differences in the size spectrum of available prey fish in perch and nonperch systems. Thus, brook trout in perch lakes may have to grow to a larger size than they do in nonperch lakes before transitioning to piscivory. Further research into the growth patterns of sympatric brook trout and yellow perch populations is necessary to determine whether the timing of the transition to piscivory is an important determinant of brook trout population density and biomass in perch lakes.

The rate of piscivory observed in perch systems was

higher than previously reported for lentic brook trout populations (Flick 1977; Fraser 1980; East and Magnan 1991; Tremblay and Magnan 1991). The high rate of piscivory raises the question of whether brook trout predation can exert top-down control on yellow perch population density. Walters and Kitchell (2001) hypothesized that predators may be capable of sufficiently reducing the density of their intraguild prey to cultivate improved conditions for juvenile predator growth and survival. The presence of piscivores can alter yellow perch abundance in lakes. For example, yellow perch density was inversely related to walleye *Sander vitreus* density in boreal lakes (Colby and Baccante 1996; Spencer et al. 2002) and the presence of northern pike *Esox lucius* significantly reduces yellow perch abundance (Rask 1983; Findlay et al. 2005). In the case of brook trout, however, yellow perch benefit from a seasonal refuge from predation in warm shallow waters. Furthermore, the threshold of yellow perch density below which nonpiscivorous-sized brook trout growth and survival increases may be lower than the potential predation effect of piscivorous brook trout. Based on the high catch rates of yellow perch and the lower abundance of brook trout in perch versus nonperch lakes, nonpiscivorous-sized brook trout do not appear to benefit from perch predation by piscivorous brook trout in the study lakes. However, before the increase in recreational fishing in the 1940s and 1950s in our study area brook trout may have been present at densities high enough to exert a significant predation effect on yellow perch populations as historical accounts suggest high brook trout abundance in our study lakes (Bice 1980).

Intraguild predation is thought to be a common

interaction among fish species with potential consequences for fish population dynamics and fisheries management (Polis and Holt 1992; Walters and Kitchell 2001). This study of ontogenetic patterns in brook trout resource use suggests brook trout and yellow perch interact as intraguild predator and prey (Figure 5) with potential consequences for brook trout abundance and benthic versus pelagic energy flow in lake food webs. Previous studies of intraguild predation among fish involved species with very different ontogenies. Prey species (e.g., reidside shiner, roach, bluegill) were characterized by limited ontogenetic diet shifts relative to predator species (e.g., rainbow trout, yellow perch, smallmouth bass *M. dolomieu*), which grew to large sizes, exploited a wide prey size spectrum, and ultimately became piscivorous. Piscivores are expected to be disadvantaged in exploiting invertebrate prey relative to nonpiscivores due to developmental trade-offs related to the shift to piscivory (Werner and Gilliam 1984; Persson 1988). Feeding performance studies indicated this was the case for rainbow trout, smallmouth bass, and yellow perch relative to their intraguild prey (Johannes and Larkin 1961; Werner 1977; Bystrom et al. 1998). This result was consistent with theoretical models that suggest the coexistence of predator and prey in intraguild predation interactions requires predators to be an inferior competitor for shared resources; otherwise, prey are excluded by the combined pressures of competition and predation (Polis et al. 1989). In the present study we found evidence for intraguild predation between two piscivores. Both species face developmental constraints associated with piscivory. However, based on differences in morphology and life history we expected yellow perch, the intraguild prey, to dominate the competitive interaction. In particular, yellow perch possess a protrusible mouth that makes feeding on small invertebrate prey more efficient (Moyle and Cech 2000). Yellow perch also have a higher temperature tolerance than do brook trout allowing them to forage in warm littoral waters that for brook trout are costly to exploit. Finally, yellow perch occur at densities 100–500 times greater than do brook trout and may dominate the interaction numerically. Recent research has focused on the possibility for alternative outcomes to intraguild predation interactions among fish species (Walters and Kitchell 2001). The present study establishes a new example of intraguild predation between two piscivores. Future research into the factors that determine the relative importance of predation versus competition to brook trout population dynamics may provide further insight into intraguild predation in fish communities.

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