Food partitioning between coexisting Atlantic salmon and brook trout in the Sainte-Marguerite River ecosystem, Quebec

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Food resource partitioning between similar-sized, sympatric Atlantic salmon *Salmo salar* and brook trout *Salvelinus fontinalis* was examined as a possible mechanism enabling their coexistence in a stream (Allaire) of the Sainte-Marguerite River ecosystem, Quebec, Canada. Fish stomach contents and invertebrate drift were collected concurrently during three diel cycles in August to September 1996. The food and feeding habits of an allopatric brook trout population in a nearby stream (Epinette) were studied for comparison. The diel feeding rhythms of the two coexisting fish species were similar. The composition of their diet, however, showed significant differences. Atlantic salmon predominantly (60–90%) fed on aquatic insects, mainly Ephemeroptera (35–60% of the diet). The brook trout mostly (50–80%) fed upon the allochthonous terrestrial insects (mainly adults of Coleoptera, Hymenoptera and Diptera) which comprised 5–40% of the stream drift. The allopatric brook trout fed opportunistically on the more abundant aquatic insects and terrestrial insects rarely formed 25% of its diet. The allopatric trout fed nearly twice as much as the sympatric brook trout during a day. The results suggest that the differences in feeding by brook trout in the two streams (with and without Atlantic salmon) are the result of inter-specific interaction with Atlantic salmon and are not related to the differences in food availability between the two streams. Food resource partitioning between Atlantic salmon and brook trout may be viewed as an adaptive response resulting in a greater exploitation of available resources and coexistence. © 2004 The Fisheries Society of the British Isles

Key words: Atlantic salmon; brook trout; competition; drift; prey selection; resource partitioning.

INTRODUCTION

The loss of some self-sustaining stocks of Atlantic salmon *Salmo salar* L. and the decline in Atlantic salmon production through much of its distributional zone (Saunders, 1981; Mills, 1989) have caused a serious concern for its conservation in the Sainte-Marguerite River (SMR), Quebec, Canada. Multiple factors operating at different scales can limit the production of Atlantic salmon

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during its freshwater residence. One important factor could be an inadequate supply of food (invertebrates) for the juvenile Atlantic salmon, especially in nutrient-poor nursery streams. Nutrient enrichment of such streams can enhance benthic algal production and thereby increase invertebrate abundance (Weng *et al.*, 2001). This in turn may subsequently improve the condition and production of salmonids (Johnston *et al.*, 1990).

Nutrient enrichment experiments in the SMR system were proposed in an earlier study (Weng *et al.*, 2001) to test if experimentally enhanced stream productivity can increase Atlantic salmon smolt production from this river. Such remedial manipulations may however, 'reverberate' through the network of biotic interactions in the ecosystem and may result in unpredictable and undesirable outcomes. For example, brook trout *Salvelinus fontinalis* (Mitchill) that also inhabits this ecosystem, could modify the impact of food base manipulations by altering the feeding conditions in the stream through competition. Any attempt to increase the productivity of streams where these closely related species coexist, should be preceded by a thorough understanding of their feeding ecology and trophic relations with each other and with the rest of the stream communities. Despite the importance of these two species to the regional economy and to the sport fishery, little is known about how these species reduce competition and become ecologically compatible in the SMR.

Competition can play a critical role in influencing the habitat selection, foraging behaviour, growth and survival of fish stream communities (Hearn, 1987; Gordon, 2000). Fluvial salmonids are usually members of small fish assemblages exploiting similar resources and hence may show ecologically significant effects from competitive interactions (Hearn, 1987; Fausch, 1998). Evidence has been provided that inter-specific interaction between native and native or non-native salmonids can influence fish growth and survival and in extreme cases, may pose a risk of the local extinction of stocks (Gibson, 1973; Gibson & Cunjak, 1986; Hearn, 1987; Fausch, 1998).

Atlantic salmon has coevolved with brook trout in North America and brown trout *Salmo trutta* L. in Europe, and often they coexist as juveniles (Gibson *et al.*, 1993; Fausch, 1998). Coexistence of guilds of similar species despite the pressures from inter-specific competition is promoted through differential use of resources (resource partitioning) along three principle niche dimensions: food, space and time (Schoener, 1986; Gordon, 2000). Consequently, the realized niche of a species becomes only a sub-set of its fundamental niche. Deducing the patterns of resource utilization and measuring the extent of niche overlap of coexisting species have become central in evaluating competition and its consequences for populations and communities (Hearn, 1987; Gordon, 2000).

Prior to proceeding with the nutrient addition experiments with an ultimate goal of enhancing Atlantic salmon smolt production from the SMR, the feeding ecology of Atlantic salmon and brook trout coexisting in this system were studied. The objective was to examine the diel patterns in feeding and the degree of overlap in food utilization between Atlantic salmon and brook trout, and the relationship of such overlap to competition. The diel food consumption and prey selection patterns of sympatric juvenile Atlantic salmon and brook trout (1+ and 2+ year age groups) were compared in relation to food availability in a stream (Allaire) during August to September 1996.

Simultaneously, the feeding ecology of an allopatric population of brook trout in a nearby stream (Epinette) was also studied. No stream with an allopatric Atlantic salmon population was available for comparison. If inter-specific competition is an important force in this system, then in sympatry Atlantic salmon and brook trout may either feed at different times or specialize on different food items. In addition to contributing to the understanding of the role played by competition in lotic ecosystems, this study would be critical in developing nutrient enrichment as an effective management tool for enhancing juvenile Atlantic salmon production in the SMR system.

MATERIALS AND METHODS

STUDY SITE

This study was conducted in two streams, Epinette and Allaire, of the Sainte-Marguerite River ecosystem located in the Saguenay region of Quebec (Fig. 1). Epinette has only brook trout while Allaire has both brook trout and Atlantic salmon. In the study site, the average density of fishes (1+ and 2+ year age groups) was 6·16 Atlantic salmon $100 \, m^{-2}$ and 7·34 brook trout $100 \, m^{-2}$ in Allaire, and 15·9 brook trout $100 \, m^{-2}$ in Epinette during the study period (August to September 1996). Study sections in the two streams were carefully chosen so as to minimize the differences in their physical attributes (*e.g.* substratum and riffle-pool pattern). The substratum was visually assessed as consisting of *c.* 10% small boulders (25–50 cm), 35% rubble (12–20 cm), 25% cobble (6–12 cm), 12% pebble (3–6 cm) and 10% coarse to fine gravel (<3 cm). Allaire had a few large boulders of 0·5–1 m diameter. Physical characteristics of the streams are given in Table I. Riparian vegetation along both streams was dominated by red maple, eastern white cedar, black spruce, white birch and grasses. Twenty-four hour collections of fish stomach contents
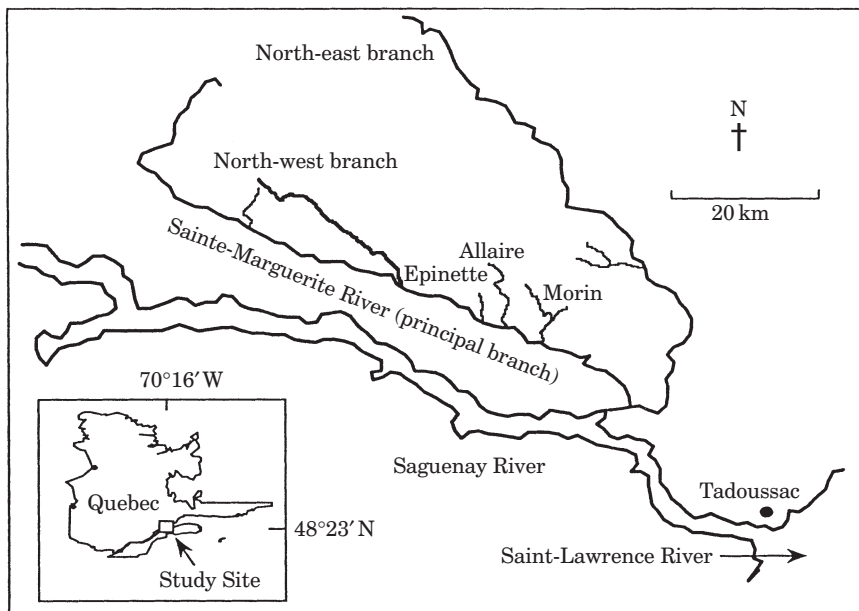

FIG. 1. Study streams (Allaire and Epinette) of the Sainte-Marguerite River system, Saguenay region of Quebec, Canada.

TABLE I. Some stream and fish attributes during the study period. Values for the stream are given as ranges and for the fish ($n = 112–210$) as means ± S.E. of all observations from three sampling occasions

	Allaire	Epinette
Stream attributes		
Width (m)	4·45–10·15	4·15–7·01
Depth (m)	0·15–0·55	0·09–0·35
Temperature (° C)	7·7–16·3	8·6–18·2
Conductivity (μS cm^{-1})	23·7–35·3	18·3–22·6
Current velocity (m s^{-1})	0·21–1·03	0·07–1·22
Fish attributes		
L_F (cm)		
Atlantic salmon	10·2 ± 0·1	
Brook trout	11·2 ± 0·2	10·2 ± 0·2
Wet mass (g)		
Atlantic salmon	12·1 ± 0·2	
Brook trout	16·5 ± 0·7	12·5 ± 0·5
Condition factor		
Atlantic salmon	1·16 ± 0·0	
Brook trout	1·09 ± 0·0	1·08 ± 0·0

and invertebrate drift were carried out on three occasions in 1996; I: 28–29 August (Allaire) and 30–31 August (Epinette), II: 9–10 September (Allaire) and 11–12 September (Epinette); III: 20–21 September (Allaire) and 22–23 September (Epinette).

DRIFT SAMPLING

Drifting macroinvertebrates were collected in three drift nets (30·48 × 30·48 cm opening, 1 m net-length, 250 μm mesh-size) placed across the width of the stream at the upper end of the fish sampling zones. The height of the water column and the water velocity (measured with Pigmy Current Meter, Model D625FM) at the net opening were recorded and nets were replaced with a new set every 2 h over the 24 h period. The drifts collected at the end of each 2 h were washed into plastic bottles and frozen at $-20°$ C for later analysis. Samples were thawed, invertebrates were identified to families where feasible, and enumerated under the microscope. Drift density (D_d) (number of invertebrates drifting 100 m^{-3} of water) was calculated following Smock (1996) as: $D_d = 100 N (3600 t W H V)^{-1}$ where, N = number of invertebrates in a sample, t = time that the net was in the stream (h), W = net opening width (m), H = mean height of water column at the net mouth (m), and V = mean water velocity at the net mouth (m s^{-1}, at 60% depth) and 3600 is the number of seconds in an hour.

FISH SAMPLING

The selected sections were fished with a backpack electroshocking unit (Model 15C, Smith-Root Inc.) at 4 h intervals, starting at 1000 h on each sampling occasion. To avoid re-shocking and disruption of fish feeding, fishing always progressed in an upstream direction. During each fishing effort, an attempt was made to capture as many fishes (minimum seven of each species) as possible within 45 min. At the end of electrofishing, fishes were brought to the shore and held in large tubs with stream water. One fish was taken out at a time and lightly anaesthetized. Fork length (L_F, to the nearest 1 mm) and wet mass (M, to the nearest 0·01 g) were recorded and stomach contents were collected

by pulsed-hydraulic stomach flushing. To extract the stomach contents, the fish was held over a funnel and stream water from a pump was flushed into its mouth. The regurgitated food was collected in a bottle attached to the funnel and frozen until analysis. The fish was placed in fresh water, revived and released into a multi-holed enclosure set within the stream. All fishes collected during the study were held in the enclosure until the end of sampling (next day) and thereafter released in the stream. No mortality was observed within the enclosure. Fishes measuring between 7 and 14 cm (1+ to 2+ year age groups) were used for this study. Water temperature was recorded each hour.

Stomach contents were thawed and analysed at the same taxonomic resolution as the drift. All contents (excluding stones, empty caddis fly cases and debris) were dried in pre-weighed aluminum pans at 60° C for 72 h to obtain a dry mass of stomach contents. Fish condition was estimated by calculating Fulton's condition factor K, $K = 100 \, M \, L_F^{-3}$, M in g and L_F in cm (Bagenal & Tesch, 1978). Gut fullness (F_t, g dry mass 100 g^{-1} wet fish mass) for each fish sampled at time t (Boisclair & Leggett, 1988) was calculated from: $F_t = 100 \, G_t \, M^{-1}$, where G_t is the dry mass of the stomach contents. Daily ration (D, g dry mass 100 g^{-1} wet mass day^{-1}) (Eggers, 1977) was calculated as:

$$D = 24 \bar{F} \, R$$

where, $\bar{F}$ is the mean gut fullness during 1 day, 24 the number of hours in a day and R is the evacuation rate per hour. The values of R at different water temperatures (T) was estimated from the equation ($R = 0.00104T^2 - 0.0095T + 0.0808$; $r^2 = 0.67$, $n = 23$) derived by F. Burton & D. Boisclair (pers. comm.) using published evacuation rates for salmonids and from their own experiments on the salmonids of the SMR system. No correction factor was used to calculate D as the differences in the mass of stomach contents at the start and at the end of the 24 h period were not significant (Amundsen *et al.*, 1999). Monte-Carlo simulations were applied to estimate the error associated with the values for daily ration (Sirois & Boisclair, 1995).

Diel similarity in the taxonomic composition between the diet of two fish species was estimated by Schoener's overlap index (Wallace, 1981) as: $O_{ij} = 1 - 0.5\Sigma_{h=1}^{n}|P_{ih} - P_{jh}|$ where n is the number of prey categories; P_{ih} and P_{jh} are the proportion of prey type h in the stomach of fish species i and j, respectively. Overlap values range between 0 (no overlap) and 1 (complete overlap). Values >0·6 are considered biologically significant. This index was used to estimate similarities between the diets of: (i) Atlantic salmon in Allaire and brook trout in Allaire (TA), (ii) Atlantic salmon in Allaire (SA) and brook trout in Epinette (TE), (iii) brook trout in Allaire (TA) and brook trout in Epinette (TE), and also (iv) between drift compositions in the two streams. The overlap was first calculated for a pair of sampling units (*e.g.* an Atlantic salmon stomach sample *v.* a brook trout stomach sample collected at the same time, paired randomly without replacement). The mean of such pair-wise overlap values was taken as an estimate of the overlap between the two comparing units. This method allowed the S.E. to be calculated and the statistical testing on the overlap estimates (Linton *et al.*, 1989; Kreivi *et al.*, 1999) to be calculated.

The diel pattern in prey preference (α) of each individual fish for a prey type (i) was determined with Chesson's (1983) index as:

$$\alpha_i = r_i n_i^{-1} \left(\sum_{j=1}^{m} r_j n_j^{-1} \right)^{-1}, \quad i = 1, 2, \ldots, m,$$

where, r_i and n_i are the number of prey type i in the stomach and in the drift, respectively; m is the number of prey categories included in the analysis (eight in this study). Preference index values (α) range between 0 (no preference) and 1 (exclusive preference) and approach m^{-1} when the diet of the predator exactly reflects the relative abundance of different prey types in the drift. The average of drift composition from two consecutive 2 h drift samples (three replicates at every sampling) collected prior to each

electrofishing interval was used for calculating Chessons' index. This should represent the available food supply for the salmonids before fishing.

STATISTICAL ANALYSES

ANOVA followed by Tukey's honestly significant difference (HSD) multiple pair-wise comparisons were used for data analyses. Data were transformed when necessary to reduce non-normality and heterogeneity of variances (Sokal & Rohlf, 1981). Log_{10}-transformed gut fullness data were back-transformed to calculate daily ration. Drift densities in two streams were compared by t-test of paired two samples for means.

RESULTS

FISH ATTRIBUTES

The fork length of fish captured for any 'fish type' (SA, TA, TE) did not vary significantly between the three sampling occasions (one-way ANOVA, F-test, $P \geq 0.37$). The average L_F and M of TA were significantly greater than those of TE (Table I; Tukey's HSD test, $P < 0.01$). The K values of brook trout in the two streams, however, were not significantly different ($P = 0.570$).

QUANTITATIVE FOOD INTAKE

A diel pattern in total number of prey consumed was not clearly apparent for SA, TA or TE [Fig. 2(a)] except on the second sampling occasion (9–10 September) when a significantly higher number of prey were consumed by fishes (both SA and TA) in Allaire between dusk and dawn (1800–0600 hours; ANOVA, log_{10}-transformed data, $P < 0.01$). Maximum number of prey consumed by TA was between 2200 and 0200 hours and by SA was between 0200 and 0600 hours (Tukey's HSD test, $P < 0.01$). Although on other sampling occasions, no diel pattern was apparent, the feeding incidence (percentage of fishes with fresh food in stomach) was lower during the day-light hours; 28–60% of SA, 18–33% of TA and 12–55% of TE had empty stomachs during 0600–1800 hours. During the low-light hours (1800–0600 hours) only 0–17% of SA, 0–25% of TA and 0–12% of TE had empty stomachs.

The number of prey consumed by TE was significantly lower than those consumed by TA only during the second sampling occasion [two-way ANOVA, $P < 0.05$, Fig. 2(a)]. This was primarily due to a significantly higher feeding activity of TA around 0200 hours (Tukey's HSD test, $P < 0.001$).

Both TA and TE did not show any significant diel difference in their gut fullness on any sampling occasion [Fig. 2(b); ANOVA, $P = 0.06–0.86$]. The SA showed a difference in their diel gut fullness only on the second sampling occasion ($P = 0.028$), which was significantly higher at 1400 hours (Tukey's HSD test, $P = 0.03$). The gut fullness and daily ration of TE were significantly higher than those of TA and SA on all sampling occasions [Figs. 2(b) and 3; one-way ANOVA, log_{10}-transformed data, $P < 0.01$]. Daily rations of TA and SA were comparable on the first sampling occasion (Tukey's HSD test, $P = 0.955$). The daily rations of the TA, however, were significantly higher
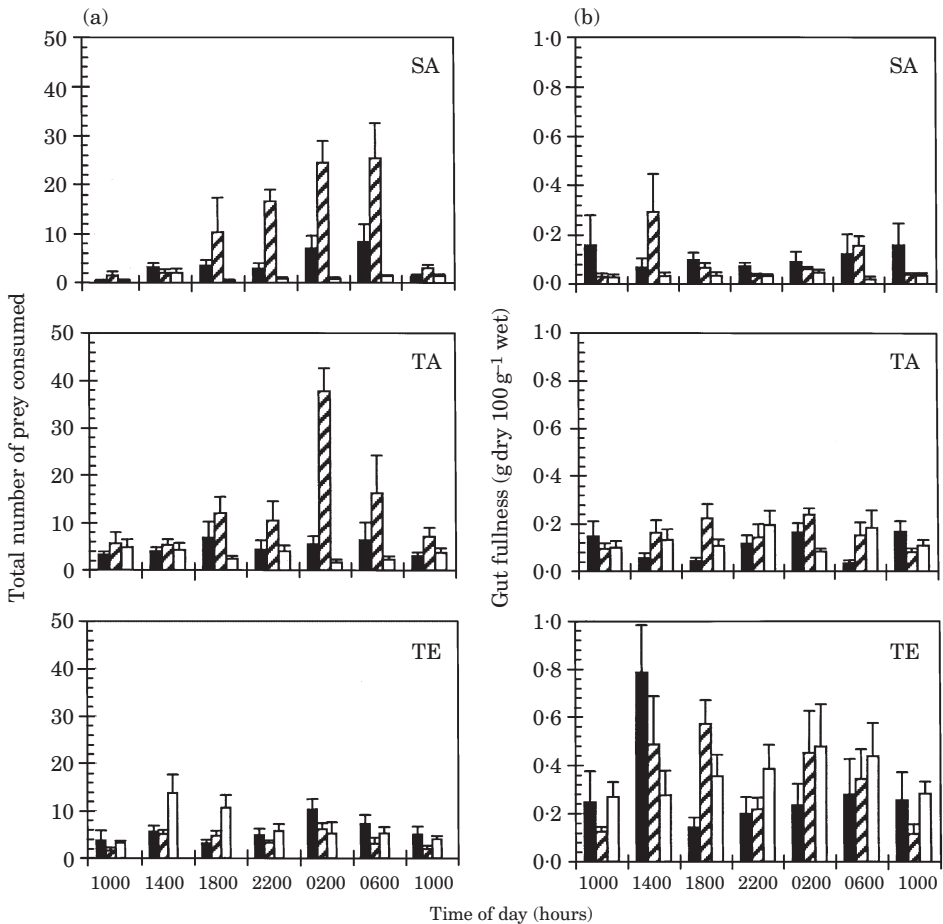
FIG. 2. Diel changes in the mean + S.E. total number of prey (all insect categories) consumed (a) and mean + S.E. gut fullness (b) for Atlantic salmon in Allaire (SA), brook trout in Allaire (TA) and brook trout in Epinette (TE), on three sampling occasions (28–31 August, ■; 9–12 September, ▨; 20–23 September, □) ($n = 7$–16).

than those of the SA on the second ($P = 0.05$) and third ($P = 0.007$) sampling occasion.

QUALITATIVE FOOD INTAKE

Both Atlantic salmon and brook trout were feeding mainly on insects. The major aquatic insect categories consumed were larvae of Ephemeroptera (Baetidae, Ephemerillidae and Heptageniidae), Plecoptera (Chloroperlidae and Perlidae), Trichoptera (Hydropsychidae, Philopotamidae and Rhyacophilidae), Diptera (Simuliidae, Tipulidae, Chironomidae and Blephariceridae), and the terrestrial insects consumed were larvae of Lepidoptera and adults of Diptera, Coleoptera, Hymenoptera and Homoptera. Other than insects, Arachnida were eaten occasionally by both species. The SA were feeding more frequently on aquatic insects than both TA and TE (Fig. 4). Among aquatic insects,
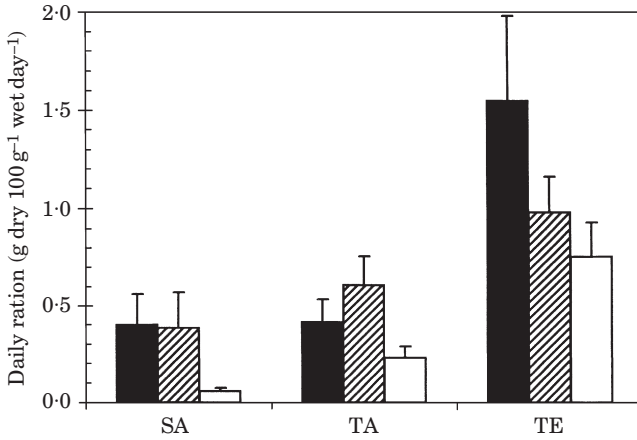
FIG. 3. Mean + S.E. daily ration estimates of Atlantic salmon in Allaire (SA), brook trout in Allaire (TA) and brook trout in Epinette (TE) on three sampling occasions (28–31 August, ■; 9–12 September, ▨; 20–23 September, □).
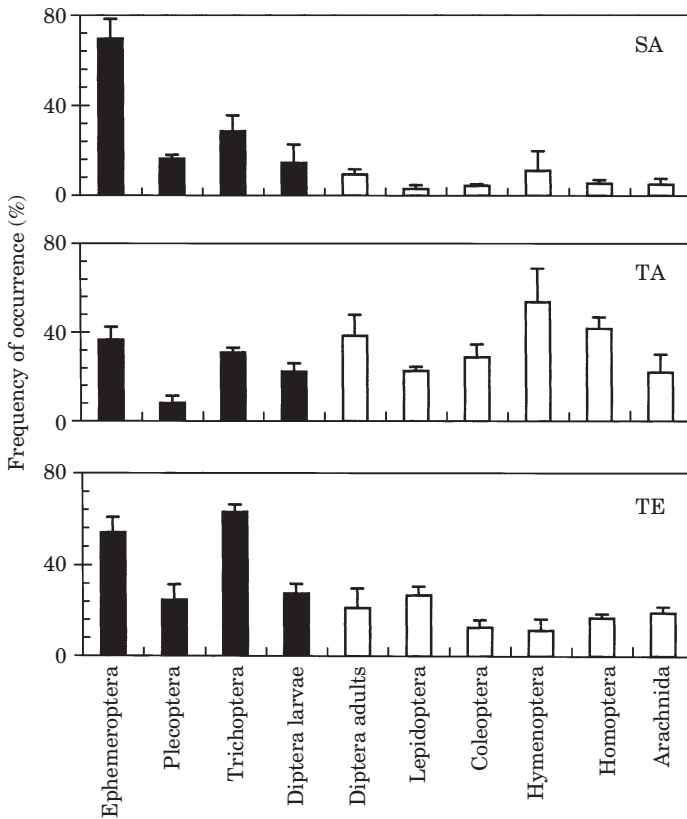

FIG. 4. Frequency of occurrence of different prey categories (expressed as percentage of all stomachs analysed, empty stomachs excluded) in the diet of Atlantic salmon in Allaire (SA), brook trout in Allaire (TA) and brook trout in Epinette (TE). ■, aquatic prey; □, terrestrial prey. Values shown are mean + S.E. of all three sampling occasions.

Ephemeroptera was most frequent (70% of the fish) in the diet of SA. Terrestrial insects were more frequent in the diet of sympatric (TA) than in the diet of allopatric (TE) brook trout.

Diel differences in the diet overlap estimates between any two 'fish types' (SA, TA and TE) were insignificant (one-way ANOVA, $P > 0.24$) on all sampling occasions. Therefore, a mean overlap value for a day (Fig. 5) was calculated using all the diel overlap values for each combination of fish types (SA and TA, TA and TE, and SA and TE). The overlap index values were considerably lower than the threshold value of 0·6 for each combination of fish types indicating that there were differences in feeding habits between brook trout and Atlantic salmon and also between two streams. This was despite the fact that drift composition was similar in the two streams (Fig. 5). The diet of SA was composed of 60–90% of aquatic insects (Fig. 6), of which Ephemeroptera made up 35–60%. The diet of TA (coexisting with Atlantic salmon) had a wider breadth and showed a clear preponderance (*c.* 50–80%) of terrestrial insects (adults of Hymenoptera, Diptera and Coleoptera). Brook trout in Epinette (without Atlantic salmon) also frequently consumed terrestrial insects (TE, Fig. 4), but these rarely made up 25% of the diet of TE (Fig. 6). The TE fed primarily (*c.* 70% of the total diet) on the autochthonous aquatic insects, Ephemeroptera and Trichoptera, in almost equal proportions. The considerable differences in the diet composition between TA and TE despite a significant similarity in drift composition (Fig. 5) in the two streams clearly indicate different feeding habits of brook trout in sympatry and allopatry.

INTAKE *V*. AVAILABILITY OF FOOD

Drift density was higher in Allaire than in Epinette on all sampling occasions, but it was significantly higher only during the second sampling occasion (*t*-test,
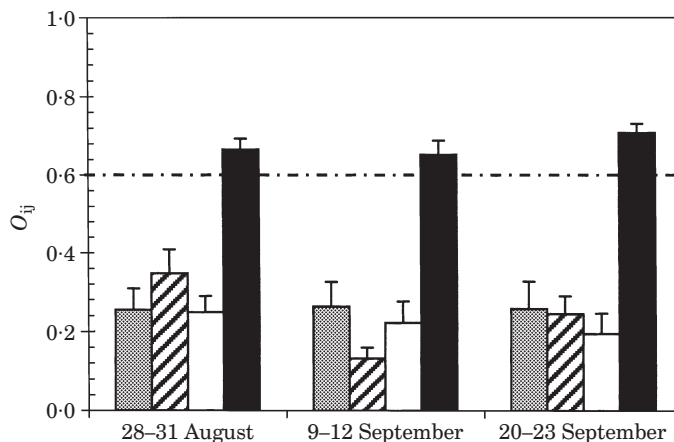

FIG. 5. Schoener's overlap index (O_{ij}) values between the diet composition of (i) brook trout and Atlantic salmon in Allaire, (TA & SA, ▨), (ii) brook trout in Allaire and brook trout in Epinette (TA & TE, ▧), (iii) Atlantic salmon in Allaire and brook trout in Epinette (SA & TE, □) and (iv) between the drift in the two streams, (■), on three sampling occasions. Values shown are average for a day. Values >0·6 (· ▬ ·) indicate significant overlap.
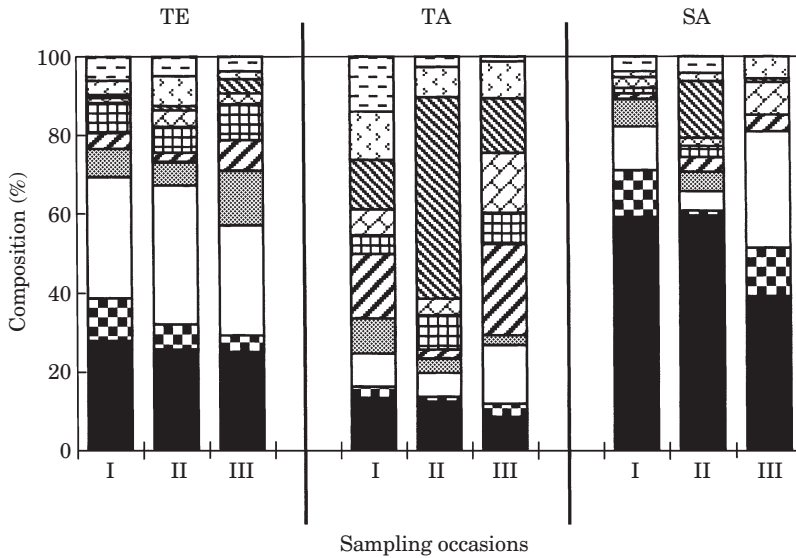
FIG. 6. Relative numerical contribution of different prey categories to the diet of brook trout in Epinette (TE), brook trout in Allaire (TA) and Atlantic salmon in Allaire (SA) on three sampling occasions (I, 28–31 August; II, 9–12 September; III, 20–23 September). Values shown are average for a day. Aquatic prey categories: Ephemeroptera, ■; Plecoptera, ▰; Trichoptera, □; Diptera larvae, ▨; terrestrial prey categories: Diptera adults, ◪; Lepidoptera larvae, ⊞; and adults of Coleoptera, ◩; Hymenoptera, ▧; Homoptera, ◳; Arachnida, ⊟.

$P < 0.01$). The total number of prey (all insect categories) consumed by TE or TA was not significantly correlated with the total (aquatic and terrestrial) drift density [Fig. 7(a) $r = 0.32$, $P = 0.19$]. The total number of prey consumed by SA, however, was significantly correlated with the total drift density ($r = 0.59$, $P = 0.01$). The utilization of aquatic insects [Fig. 7(b)] by fishes reflected its availability more closely in the stream Epinette (TE, $r = 0.72$; $P = 0.0008$) than Allaire (TA, $r = -0.06$, $P = 0.83$; SA, $r = 0.35$, $P = 0.15$). These patterns indicated that TE were feeding opportunistically on the more abundant prey types and showed a selection for Trichoptera amidst aquatic prey and Lepidoptera amidst terrestrial prey (Fig. 8). The TA showed greater preference for the terrestrial components (such as Hymenoptera and Coleoptera, Fig. 8) which made up <40% of the drift. The TA did not actively select any of the aquatic insects, although they made up 60–95% of the drift. The SA were selective and had a strikingly greater preference for Ephemeroptera.

DISCUSSION

There are two theories regarding the feeding chronology of salmonids: (1) salmonids are largely diurnal feeders, maximizing their net energy input during the day when they can detect prey more efficiently (Walsh *et al.*, 1988; Fraser & Metcalfe, 1997); (2) salmonids are thought to be crepuscular and nocturnal foragers (Amundsen *et al.*, 1999, 2000; Kreivi *et al.*, 1999). Yet other studies have observed no particular pattern in feeding (Forrester *et al.*, 1994). Studies
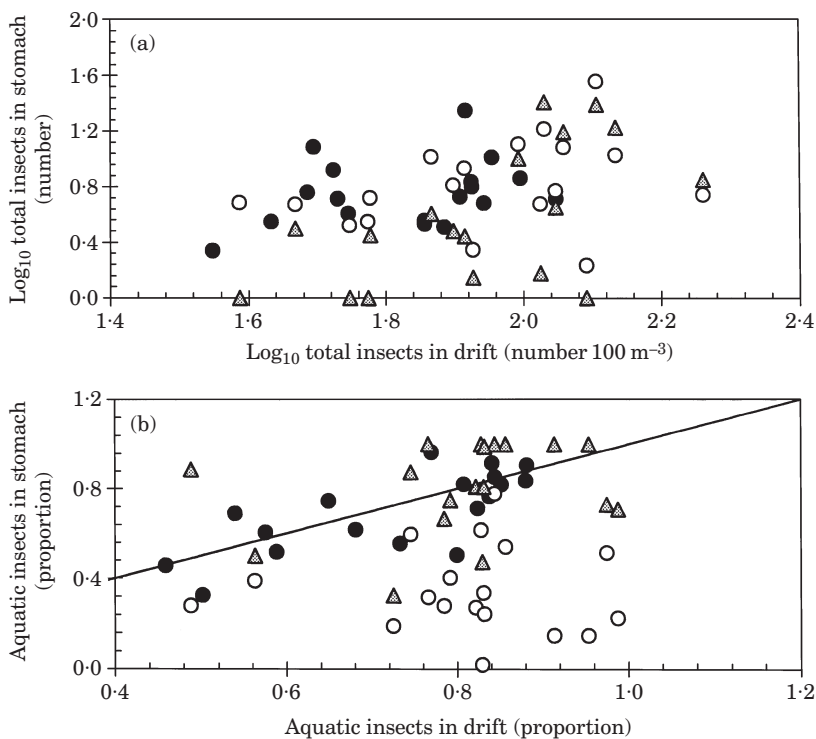
FIG. 7. (a) Total number of insects (all aquatic and terrestrial categories) consumed by fishes in relation to total insect density in the drift and (b) proportion of aquatic insects consumed by fishes in relation to proportion of aquatic insects in the drift (——, 1 : 1 ratio), for brook trout in Epinette (TE, ●), brook trout in Allaire (TA, ○) and Atlantic salmon in Allaire (SA, ▲). Values shown are mean of each diel sampling interval for all three sampling occasions.

on the feeding chronology of coexisting salmonids are rare. In this study, salmonids, both sympatric and allopatric, did not show any particular diel pattern in feeding intensity (amount of food in stomach) except on one occasion when the sympatric Atlantic salmon and brook trout in the stream Allaire, fed predominantly during the crepuscular and dark hours of the day. Nevertheless, on all sampling occasions the feeding incidence (percentage of fishes with fresh food in stomach) was lower during the day-light hours for both sympatric and allopatric salmonids. More importantly, this study suggests that there was no partitioning of 'time of feeding' between Atlantic salmon and brook trout in sympatry, *i.e.* they were not foraging at different times to minimize inter-specific interaction.

Although there were some similarities in the diet composition of coexisting Atlantic salmon and brook trout, the overlap was small irrespective of the time and day of sampling. They partitioned the available food by utilizing different food items as seen for various species of coexisting brook and brown trout and Atlantic salmon (Gibson & Cunjak, 1986; Gibson *et al.*, 1993). Brook trout were 'generalist' feeders having a wider diet breadth, with prey of terrestrial origin being more important in terms of both their frequency in the diet and
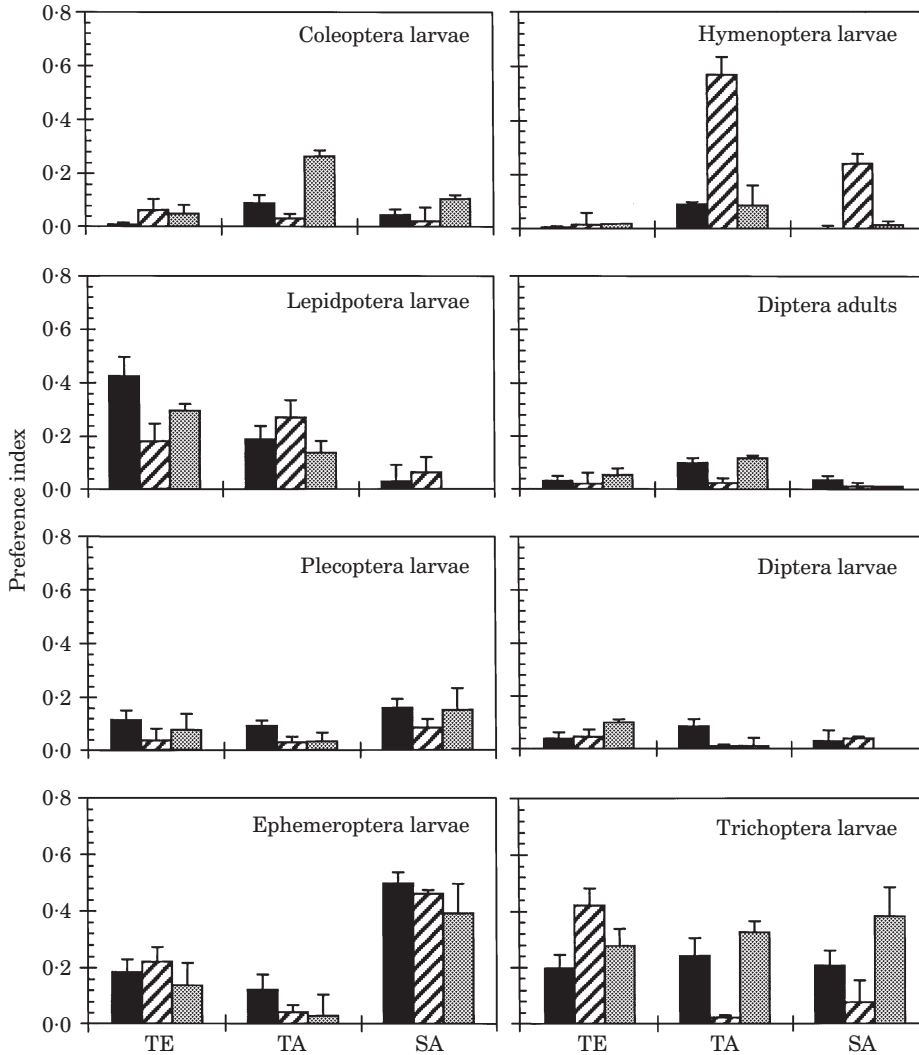
FIG. 8. Chesson's preference index (α) values (average for a day) for various insect categories for brook trout in Epinette (TE), brook trout in Allaire (TA) and Atlantic salmon in Allaire (SA) on three sampling occasions (28–31 August, ■; 9–12 September, ▨; 20–23 September, ▩). Values >0·125 indicate preference.

their numerical contribution to the total number of prey consumed. On the other hand, Atlantic salmon selected aquatic prey over terrestrial, had a narrow diet breadth, and 'specialized' on Ephemeroptera.

The brook trout populations in the two streams had pronounced differences in their food intake and feeding habits. The sympatric brook trout had a wider diet breadth compared to the allopatric brook trout. The TA used much of the resource spectrum and consumed mainly prey of terrestrial origin. On the other hand, the TE fed opportunistically on the most abundant aquatic stages of insects. Only on one occasion did TE consume fewer numbers of prey than TA.

On all sampling occasions, TE consumed more of larger prey (*e.g.* Trichoptera), which is probably why the gut fullness values for TE were higher than those for TA. Also, TE had a daily ration twice as much as TA. It is possible that using the same gastric evacuation pattern for all prey types to calculate the evacuation rate is not accurate when comparing the daily ration of the two brook trout populations feeding on different food types. This is unlikely, however, because the equation used to calculate the evacuation rate is based on salmonids feeding on diverse food types from small chironomids to large trichopterans (F. Burton & D. Boisclair, pers. comm.).

The disparities in the diet quality of brook trout in allopatry (Epinette) and sympatry (Allaire) suggest that competition played an important role in generating the observed patterns of diet shift of brook trout in the presence of Atlantic salmon. The similarity of the two coexisting species food utilization patterns on one axis (time of feeding) was offset by pronounced dissimilarity of their patterns along another (type of food taken) helping coexistence. There is no certainty that all factors other than the absence of Atlantic salmon were constant and comparable in these two streams on all sampling occasions. Nevertheless, the differences in food availability between the two streams do not explain the variations in the diet composition of the two brook trout populations.

Differences in the diet composition as seen in the present study between coexisting salmonids have been associated with a spatial segregation between species caused by inter-specific competition (Gibson & Cunjak, 1986; Gibson *et al.*, 1993; Fausch, 1998). Closely related species in sympatry often do not utilize the full range of their ecological potential, but limit themselves to their 'ecological optimum niche' where they are best adapted and are most likely to have a competitive advantage over other species (Hearn, 1987). Behavioural observations and field experiments suggest that Atlantic salmon are more aggressive and dominant over brook trout in inter-specific encounters in riffles (Gibson, 1973, Hearn, 1987; Gibson *et al.*, 1993; Rodríguez, 1995). In sympatry with Atlantic salmon, brook trout are displaced from the riffles towards the pools where they compete more successfully with the Atlantic salmon. In the absence of Atlantic salmon, brook trout expand their habitat by occupying faster-water riffles (Gibson *et al.*, 1993).

Although habitat selection was not specifically examined in this study, careful observations of where the fishes were caught during electrofishing, indicated that Atlantic salmon in Allaire mostly occupied riffles and were rarely found in the pools. It appeared, however, that brook trout (1+ and 2+ year) were randomly dispersed and occupied a wide array of stream habitats. They were often electrofished from fast-flow riffles which are usually occupied by Atlantic salmon under sympatric conditions (Gibson *et al.*, 1993; Rodríguez, 1995). Atlantic salmon and brook trout were frequently caught together from the same riffle. Observations during electrofishing did not indicate any clear-cut habitat segregation between Atlantic salmon and brook trout in sympatry. Also, no difference in the habitat occupied by allopatric and sympatric brook trout was apparent. The study sections had few pools, which were mostly occupied by larger brook trout (>16 cm; $\geq$3+ year age group). These streams are nutrient-poor (total phosphorus concentration was *c.* 5 μg l^{-1}, total nitrogen concentration between 150 and 220 μg l^{-1}) with very low invertebrate densities

(*e.g.* at peak drift these streams have only *c.* 4 individuals m^{-3} of Ephemeroptera) (Weng *et al.*, 2001). In a low-productive environment, and under conditions where the brook trout's secondary habitat during competition (pools) (Gibson, 1973, Gibson *et al.*, 1993, Rodríguez, 1995) are few, it is possible that young brook trout may have to occupy and forage in all possible habitats to meet their essential energy demands. A broader niche of brook trout for both habitat use and food choice perhaps maximizes their returns per unit energy expenditure. To identify with certainty the microhabitat use by brook trout in allopatry and sympatry, and to verify the observations during electrofishing, it would be essential to carry out behavioural observations in the field through SCUBA diving or by snorkelling.

Insignificant niche overlap such as seen in this study between closely related coexisting species can be related to competition when resources are limiting (Schoener, 1986; Gordon, 2000). The initial nutrient enrichment experiment to increase the invertebrate production conducted in the SMR system suggests that these streams are nutrient poor and have a lower supply of invertebrates relative to salmonid demand (Weng *et al.*, 2001). Subsequent nutrient addition experiments with the ultimate objective of increasing Atlantic salmon smolt production in the SMR, would enhance the abundance of the grazer, Ephemeroptera, which is the major food of Atlantic salmon as shown in this study. Furthermore, the increased insect abundance may produce a 'competitive release' and consequently a greater diet similarity between sympatric and allopatric brook trout populations.

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