Diel foraging in relation to available prey in an Adirondack Mountain stream fish community

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Abstract

The diets of the fish community of Trucka Brook, a small stream located in the central Adirondack Mountains in northern New York, were examined in relation to the bottom fauna and invertebrate drift. Measures of overlap were calculated between the diets of each fish species examined, brook trout *(Salvelinus fontinalis)*, blacknose dace *(Rhinichthys atratulus)*, creek chub *(Semotilus atromaculatus)* and pearl dace *(Semotilus margarita)*. Overlap was also examined between the fish diets and bottom and drift samples. Blacknose dace, pearl dace and brook trout had the most similar diets which were closely associated with the benthos. Creek chub had the most distinctive diets which did not compare well with any other fish species during either diurnal or nocturnal periods. The mayfly nymph *Litobranchia recurvata* was the most abundant bottom invertebrate and was the major prey of benthic feeding fishes. The invertebrate drift did not compare favorably with any of the fishes' diets because of the predominance of large cased limnephilid larvae (primarily *Psychoglypha* sp.) which were not readily consumed by fish.

Introduction

The relationship of available food to the diets of a particular fish species or two or more coexisting fishes in lotic ecosystems has been examined in detail (Elliott 1973; Griffith 1974; Mendelson 1975; Allan 1978; Johnson & Ringler 1980). Only a few studies (Zaret & Rand 1971; Mancini *et al.* 1979), however, have examined the diets of an entire stream fish community in relation to available prey, possibly because of the diverse nature of many fish communities. In a study examining the feeding relationships of four species of *Notropis*, Mendelson (1975) reported that approximately 26 additional fish species occurred in the stream. In the community studies, Zaret & Rand (1971) and Mancini *et al.* (1979) each examined the diets of nine fish species.

We examined the diets of brook trout *(Salvelinus fontinalis)* blacknose dace *(Rhinichthys atratulus)*, creek chub (Semotilus atromaculatus) and pearl dace *(Semotilus margarita)*, which are all major components of the lotic fish fauna of the Adirondack Mountains in northern New York. Although a great volume of ecological information is available for each of these species, no studies have examined this specific species assemblage as a stream fish community. The purpose of this investigation was to examine interspecific overlap in diet as well as diet composition in relation to available food in the environment within a relatively small fish community diurnal and nocturnal periods.

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Materials and methods

Collections of both fish and invertebrates were made on 19–20 September 1980 in Trucka Brook, a small stream located in the central Adirondack Mountains in Essex County, New York (44°01′N; 74°13′W). The stream has a low gradient and originates from impounded water created by the dam building activities of beaver *(Castor canadensis).* The study area of Trucka Brook consisted of a 200 m meadow section which had a sand, gravel and muck substrate, an average width <2 m, and no major vegetative cover other than tall sedges (*Carex* spp.). Water temperatures ranged from 7.8 to 12.2 °C during the study.

Samples were taken at 0600 h and 1800 h in order to reflect both diurnal and nocturnal differences in fish feeding and invertebrate drift. Six Surber samples (30.5 cm²; mesh size 0.75 mm) were used to quantify the bottom fauna and three drift nets (aperture 30.5 cm × 30.5 cm; mesh size 0.60 mm) set for 12 h (i.e. 0600–1800 h; 1800–0600 h) were used to quantify the drift during each sampling interval. Drift nets were set at the upstream end of the study section at a point where three nets intercepted the entire flow of the stream. Sunrise occurred at 0649 h and sunset at 1906 h EST during the study.

Fish were collected in traps and with seines. Immediately upon collection fish were slit and placed in 10% formalin. Benthic samples were preserved in 5% formalin in the field. In the laboratory fish were measured (total length in millimeters) prior to having their stomachs removed. For the three species of cyprinids which lacked true stomachs (i.e. blacknose dace, creek chub, pearl dace) the contents of the anterior one-third of the digestive tract were used to quantify their diets since this represented the most recent material ingested. Aquatic invertebrates from both fish stomachs and benthic samples were generally identified to the lowest possible taxon whereas terrestrial invertebrates were identified to order. Dry weight estimates (24 h at 105 °C) were derived for invertebrate taxa in order to quantify their contribution in the benthic samples and in the fish diets.

Measures of overlap between fish diets and benthic samples were calculated using the equation of Morisita (1959) later modified by Horn (1966):

$$C_\lambda = \frac{2\sum_{i=1}^{s} X_i \cdot Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where C_λ = overlap coefficient,
S = food categories,
X_i = proportion of the total diet of species X contributed by food category i,
Y_i = proportion of the total diet of species Y contributed by food category i.

Investigators using this formula generally consider a value ⩾0.60 to indicate overlap (Zaret & Rand 1971; Vaught & Stewart 1974; Fuller & Stewart 1979; Johnson & Ringler 1980).

Results

A total of 259 fishes were collected during the course of this investigation (Table 1). Creek chub and blacknose dace were the predominant fishes in Trucka Brook with brook trout and pearl dace being somewhat less abundant. Although some difference in diet composition between large and small individuals of some species was suggested, especially blacknose dace and creek chub, it was decided to examine only interspecific diet relationships.

The predominant invertebrates colleted in the diurnal bottom samples were the ephemerid mayfly

Table 1. Number of fish examined, average length (total length in millimeters), and size range for each fish species during diurnal and nocturnal sampling intervals from Trucka Brook, Essex County, New York.

Diurnal Group	No.	Avg. length	Size range
Blacknose dace	46	53.7	39– 85
Brook trout	10	89.5	55–160
Creek chub	66	73.9	43–139
Pearl dace	15	66.0	57– 79
Nocturnal Group	**No.**	**Avg. length**	**Size range**
Blacknose dace	49	49.9	29– 78
Brook trout	10	98.6	61–162
Creek chub	44	65.0	44–138
Pearl dace	19	67.5	55– 83

nymph *Litobranchia recurvata* McCafferty and dragonfly nymph *Cordulegaster maculata* Selys which composed 43.3% and 18.1% respectively of the benthic standing crop (Table 2). The diurnal drift of Trucka Brook was dominated by the limnephilid caddisfly larvae *Psychoglypha* sp., which contributed 58.9% of the drift. Terrestrial invertebrates, predominantly hymenopterans (13.1%) and coleopterans (8.2%), made up 30.9% of the diurnal drift (Table 2). Blacknose dace fed heavily on the mayfly nymphs *L. recurvata* (22.7%) and *Paraleptophlebia* sp. (14.2%) and chironomid larvae (14.8%) during the day. Blacknose dace did not readily consume terrestrial invertebrates at this time. Brook trout fed heavily on *L. recurvata* (33.0%), *Psychoglypha* sp. (16.1%), phryganid caddisfly larvae (14.1%) and terrestrial annelids (14.1%) (Table 2). Creek chub primarily utilized terrestrial invertebrates during the day. Nymphs of *C. maculata* were the principal aquatic invertebrate eaten by creek chub. Pearl dace fed chiefly on *L. recurvata* (49.1%) but also consumed such unique items as sphaeriids (13.1%) and filamentous algae (4.9%) (Table 2).

At night, *L. recurvata* and *C. maculata* were again the primary components of the bottom fauna, comprising 36.2% and 24.7% of the benthic standing crop (Table 3). Caddisfly larvae, principally

Table 2. Percent dry weight composition of diurnal benthic samples and fish stomachs. Values are given only for those taxa which contributed at least 2% to one of the benthic or diet categories.

	Bottom	Drift	Blacknose dace	Brook trout	Creek chub	Pearl dace
Aquatic taxon						
Decapoda	10.6	–	–	–	–	–
Ephemeroptera						
Baetidae	–	0.7	7.0	–	–	1.5
Ephemerellidae	2.5	0.5	1.5	–	0.5	–
Ephemeridae	43.3	6.8	22.7	33.0	1.4	49.1
Leptophlebiidae	3.1	–	14.2	4.0	4.3	–
Unidentified	–	1.0	0.4	–	0.5	3.3
Odonata						
Cordulegastridae	18.1	–	–	–	12.5	–
Trichoptera						
Hydropsychidae	3.1	–	5.4	4.9	0.9	–
Hydroptilidae	–	–	0.3	–	0.1	4.6
Limnephilidae	2.7	58.9	6.2	16.1	1.9	–
Phryganeidae	2.4	–	4.9	14.1	4.4	10.6
Polycentropodidae	–	–	4.0	2.2	0.6	–
Diptera						
Ceratopogonidae	–	–	6.5	–	1.4	1.6
Chironomidae	1.0	0.4	14.8	0.2	1.6	2.0
Tipulidae	10.3	–	4.8	2.9	7.2	–
Mollusca						
Sphaeriidae	–	–	–	–	–	13.1
Filamentous algae	–	–	–	–	–	4.9
Miscellaneous	2.4	0.8	4.0	1.6	1.7	–
Total aquatic	100.0	69.1	94.5	79.0	39.0	90.7
Terrestrial taxon						
Annelida	–	–	1.5	14.1	21.0	–
Coleoptera	–	8.2	–	–	2.3	4.1
Diptera	–	5.3	0.2	–	10.2	–
Hemiptera	–	2.7	–	–	4.9	2.5
Hymenoptera	–	13.1	0.9	–	16.4	–
Lepidoptera	–	–	0.7	6.9	4.1	2.7
Miscellaneous	–	1.6	–	–	2.1	–
Total terrestrial	0.0	30.9	3.3	21.0	61.0	9.3

Table 3. Percent dry weight composition of nocturnal benthic samples and fish stomachs. Values are given only for those taxa which contributed at least 2% to one of the benthic or diet categories.

	Bottom	Drift	Blacknose dace	Brook trout	Creek chub	Pearl dace
Aquatic taxon						
Ephemeroptera						
Baetidae	–	1.8	0.7	7.0	0.4	0.8
Ephemerellidae	4.4	4.3	2.6	–	0.9	–
Ephemeridae	36.2	7.4	38.0	42.8	14.5	42.9
Leptophlebiidae	5.0	3.0	14.5	0.9	6.6	8.2
Unidentified	–	–	4.5	1.3	4.9	6.5
Odonata						
Cordulegastridae	24.7	3.3	–	–	13.3	–
Trichoptera						
Hydropsychidae	5.5	21.4	14.0	1.0	3.5	2.4
Limnephilidae	3.0	31.6	–	–	1.9	7.8
Philoptamidae	0.4	0.8	0.7	3.5	1.4	6.9
Phryganeidae	4.6	1.3	–	0.6	7.5	–
Polycentropodidae	–	–	2.9	1.3	–	–
Diptera						
Ceratopogonidae	–	–	1.5	–	2.4	3.1
Chironomidae	1.1	0.3	10.6	8.3	1.8	8.3
Dixidae	–	1.0	–	–	1.7	–
Simuliidae	1.4	2.6	0.6	–	–	–
Tabanidae	4.9	–	–	2.9	–	0.4
Tipulidae	7.2	6.9	7.6	1.4	6.7	3.3
Teleosti						
Rhinichthys atratulus	–	–	–	–	9.4	–
Miscellaneous	1.6	6.9	1.3	0.9	4.9	3.8
Total aquatic	100.0	85.7	100.0	71.9	81.8	94.4
Terrestrial taxon						
Annelida	–	–	–	–	5.7	3.2
Arachnida	–	0.7	–	6.4	–	–
Diptera	–	1.2	–	4.8	5.4	1.3
Hemiptera	–	–	–	7.9	0.1	–
Hymenoptera	–	2.2	–	5.8	3.8	–
Lepidoptera	–	2.9	–	2.3	0.9	1.1
Miscellaneous	–	0.4	–	0.9	2.3	–
Total terrestrial	0.0	7.4	0.0	28.1	18.2	5.6

limnephilids (31.6%) and hydropsychids (21.4%) dominated the nocturnal drift of Trucka Brook. Terrestrial invertebrates composed only 7.4% at this time. Mayfly nymphs, principally *L. recurvata* and *Paraleptophlebia* sp., were generally the major prey in the diet of all fish species examined at night (Table 3). With the exception of brook trout, utilization of terrestrial invertebrates by Trucka Brook fishes was substantially reduced at night. This is not surprising, however, considering that terrestrials contributed only 7.4% of the nocturnal drift compared to 30.9% of the diurnal drift. Overall terrestrial invertebrate biomass in the nocturnal drift was only 30% of that observed during the day. Additional major prey taxa in the nocturnal diet of Trucka Brook fishes included hydropsychids, phryganids, chironomids and tipuliids. Predation on blacknose dace by two large creek chub was the only incidence of piscivority observed (Table 3).

Measures of overlap were calculated between fish diets and benthic samples for the diurnal and nocturnal sampling periods (Table 4). During the day 6 of 14 comparisons exceeded the suggested level indicating overlap (i.e. 0.60). At night 7 of 14 comparisons were greater than 0.60 and overall nocturnal ($\bar{X} = 0.664$) comparisons were higher than diurnal

Table 4. Diurnal and nocturnal overlap values (C_λ) obtained when comparing fish diets and benthic samples.

		NOCTURNAL					
		Bottom	Drift	Blacknose dace	Creek chub	Pearl dace	Brook trout
DIURNAL	Bottom	–	–	0.770	0.700	0.780	0.751
	Drift	–	–	0.376	0.339	0.356	0.211
	Blacknose dace	0.685	0.220	–	0.583	0.916	0.842
	Creek chub	0.221	0.175	0.222	–	0.572	0.520
	Pearl dace	0.820	0.115	0.616	0.079	–	0.912
	Brook trout	0.727	0.416	0.700	0.343	0.772	–

($\bar{X} = 0.470$). Brook trout, blacknose dace and pearl dace had the most similar diets, which were all closely associated with the composition of the bottom fauna. The composition of the drift did not compare well with any of the fishes' diets during either diurnal or nocturnal periods. Overall the diet of brook trout was most closely associated with the drift (0.314). However, of the fish species examined, the diet of brook trout compared least favorably with the drift at night (0.211).

The diet of brook trout (0.605) compared most favorably with the other fish species during the day (Table 4). At night, when diet overlap among Trucka Brook fishes was greatest (nocturnal $\bar{X} = 0.724$, diurnal $\bar{X} = 0.455$), the diets of pearl dace (0.800), blacknose dace (0.780) and brook trout (0.758) were those most closely associated with the other fishes. Overall, the diets of brook trout (0.682), blacknose dace (0.647) and pearl dace (0.645) overlapped the most with the rest of the stream fish community whereas creek chub (0.387) overlapped the least (Table 4).

Discussion

The low overlap values obtained when comparing the fish diets to the drift were surprising. The major cause of this was the dominance of *Psychoglypha* sp. larvae in both the diurnal and nocturnal drift. This taxa was not readily consumed by Trucka Brook fishes and was relatively scarce in the bottom samples. We measured the specimens of *Psychoglypha* sp. from the drift samples and found them to average 20 mm (range 16–25 mm). However, their wooden cases averaged 41 mm (range 29–47 mm) in length. Wiggins (1977) cites maximum lengths of 26 mm for larvae and 43 mm for the cases of *Psychoglypha* sp. We also measured some of the larger specimens of *L. recurvata* from fish stomachs and found them to average 21 mm (range 16–24 mm). Since *Psychoglypha* sp. larvae and large *L. recurvata* nymphs were approximately the same size, there was no apparent reason, apart from the large size of the case of *Psychoglypha* sp., to explain the differential utilization of these potential prey by virtually the entire Trucka Brook fish community. The only fish species to substantially utilize *Psychoglypha* sp. was brook trout during the day. The larvae were eaten by three fish averaging 132 mm (range 104–160 mm) and comprised 16.1% of the diet (Table 2). Since only 5% of the fishes collected from Trucka Brook during this study exceeded 120 mm it seems likely that because of the large size of its case, *Psychoglypha* sp., although abundant in the drift, may be available to only a small portion of the stream fish community.

We reexamined the diet versus drift associations by eliminating the family Limnephilidae (primarily *Psychoglypha* sp.) from the drift data (Table 5). The diet versus drift association was increased for each of the four fish species. The diet of creek chub was found to be most closely associated with the drift (0.458); the overlap value was increased 78% by removing limnephilids from the drift data. The feeding of creek chub generally mirrored the drift in that terrestrial invertebrates dominated the diet during the day and aquatic invertebrates at night (Tables 2–3). Overall, the removal of limnephilids from the drift taxa increased diet versus drift overlaps from 20 to 78% for all fish groups with a mean increase of 47% (Table 5).

Interspecific diet overlap comparisons revealed that creek chub had the most distinctive diet of the

Table 5. Average overlap values ($C\lambda$) (and percent increase) obtained when comparing fish diets with drift samples with and without the prey taxa Limnephilidae.

Comparison (versus drift)	W/Limnephilidae	WO/Limnephilidae	% increase
Brook trout	0.314	0.376	20
Blacknose dace	0.298	0.391	31
Creek chub	0.257	0.458	78
Pearl dace	0.236	0.393	67
Average	0.276	0.405	47

four species of Trucka Brook fishes. Furthermore creek chub was the only fish species to exhibit substantial diel variation in diet composition. During the day creek chub fed heavily on terrestrial invertebrates but at night they switched to aquatic invertebrates. In addition, creek chub, especially large individuals, were the only species to utilize *C. maculata* which were a major benthic component. Investigators examining the diet of creek chub report that the minnow is an opportunistic feeder which feeds on both drifting and benthic organisms (Barber & Minckley 1971; Copes 1978; Newsome & Gee 1978). Our results certainly support the theory that creek chub is an opportunistic feeder since in Trucka Brook it was the only species to feed equally on the bottom (0.461) and drift (0.458) (minus limnephilids). Little difference in stomach fullness occurred between the diurnal and nocturnal sampling periods.

Only minor diel variation in diet composition was observed for the other fish species in Trucka Brook. Mayfly nymphs (principally *L. recurvata*) and trichopteran larvae were eaten both at night and during the day. The diet of blacknose dace was almost entirely benthic in origin and compared well with earlier food habit information on the species (Breder & Crawford 1922; Traver 1929; Gibbons & Gee 1972). Stomach fullness at 0600 h was approximately twice that at 1800 h. Pearl dace have been reported to feed on a wide variety of prey, both aquatic and terrestrial, and have been observed to utilize sphaeriids (Stasiak 1978) and filamentous algae (McPhail & Lindsey 1970) as found in our study. Pearl dace appeared to feed throughout the 24 h period; however, stomach fullness at 1800 h was only 83% of that at 0600 h.

A great volume of information exists on the feeding ecology of stream brook trout in relation to available food in the environment. McClain (1976) and Allan (1978) showed that the diet of brook trout was more closely correlated with the drift than with the benthos. Further exploring the relationship of invertebrate drift to brook trout feeding, Griffith (1974) and Allan (1981) believe that trout are selective in their utilization of drifting prey. McClain (1976), however, suggests that brook trout are non-selective in their utilization of drifting invertebrates. In Trucka Brook, brook trout preyed heavily on *L. recurvata* which was the major benthic invertebrate but which had a low drift rate. Because of this, the diet of trout was more closely associated with the bottom fauna than with the drift fauna. These data suggest that brook trout may be more plastic in their mode of foraging than previously thought and may be either drift or benthic feeders depending upon available prey, coexisting fishes and possibly stream order. Stomach fullness at 0600 h was only 80% of that at 1800 h, indicating a diurnal feeding peak which has previously been demonstrated for brook trout (McClain 1976; Allan 1981).

Undoubtedly, the habitat distribution of fishes in lotic environments affects their mode of foraging and hence the types of prey they consume. The habitat distribution of a species may be altered by the numbers and kinds of coexisting fishes. Griffith (1974) found that the diets of yearling and older brook trout and cutthroat trout *(Salmo clarki)* differed somewhat in allopatric situations and these differences increased in sympatry. Mendelson (1975) suggested that the variation in diet composition he observed in four sympatric species of *Notropis* spp. was principally the result of differences in space utilization. From his observations he theorized that the mode of foraging by predatory fish is more likely the result of selective pressures from other fish utilizing the same food supply than from the unique characteristics of the prey themselves.

Hartman (1965) and Allee (1974) found that subyearling coho salmon *(Oncorhynchus kisutch)* influenced the habitat selection of subyearling steelhead trout *(Salmo gairdneri)* in streams. Johnson & Ringler (1980) showed that, in sympatry, coho salmon occupied pools and fed from the drift whereas steelhead (rainbow) trout occupied riffles and fed mainly from the benthos. In allopatry, however, Tippets & Moyle (1978) reported that juvenile rainbow trout fed predominantly on the drift. These data suggest that variation in habitat distribution because of social interaction among fish species can influence the mode of feeding of a species. Since the bottom feeding tendencies of brook trout in Trucka Brook were in disagreement with the previous literature, it is possible that their habitat distribution may have been influenced by any one or a combination of the other species present. However, it seems just as reasonable to assume that brook trout as well as blacknose dace and pearl dace were simply feeding on the most abundant prey available, *L. recurvata,* which had a low drift rate.

Summary

The partitioning of food resources among three of the four fish species that occur in Trucka Brook was minimal during both diurnal and nocturnal periods. Blacknose dace, pearl dace and brook trout had similar diets which were all closely associated with the composition of the bottom fauna. Diet overlap among the four species was substantially higher at night ($\bar{X} = 0.724$) than during the day ($\bar{X} = 0.455$). The invertebrate drift did not compare well with any of the fishes' diets because of the predominance of large-cased limnephilid larvae (primarily *Psychoglypha* sp.) which were not readily consumed by fish. When eliminating limnephilids from the drift data, the diet versus drift overlap was substantially increased for each fish species. Diel variation in diet composition was greatest for creek chub as they fed mainly on terrestrial invertebrates during the day and aquatic invertebrates at night.

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