THE UNIVERSITY OF MANITOBA

FORAGING BEHAVIOR OF BROOK STICKLEBACK, *CULAEA INCONSTANS* (KIRTLAND), OPTIMIZATION OF TIME, SPACE AND DIET

by

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Abstract

This study was an investigation of the feeding strategies of brook stickleback, *Culaea inconstans* (Kirtland), and an assessment of its foraging efficiency in light of optimal foraging theory.

Brook stickleback were abundant in the vegetated stream margins of the Bog and Rennie Rivers, southeastern Manitoba. Stickleback were diurnal foragers, relying predominantly on vision for prey detection. Feeding intensity was greatest in June although prey were most abundant in August. Age 0 fish consumed a greater proportion of food per g body weight than age 1+ fish. Both cohorts were carnivorous, consuming crustaceans, annelids, arachnids, insect larvae and fish eggs and larvae. Stickleback selected certain taxa: chironomid larvae, Sididae, and Bosminidae, and particular size classes within taxa. Age 0 fish selected smaller food items than age 1+ fish, and both age classes consumed prey smaller than they were morphologically capable of handling.

The foraging behavior of brook stickleback is interpreted as a sequence of five phases: swim, hover, aim, dart and handle. Stickleback are capable of modifying feeding behavior depending on the distribution and abundance of prey. Food items on the substrate were consumed most frequently (78% of the feeding bites). The searching

response (swim and hover) was excluded in 32.8% of the feeding patterns. Of the sequences including swim, 34% were followed by hover, 60.5% omitted hover and 5.5% omitted both hover and aim. A large proportion of hover and aim phases (47.9% and 40.4% respectively) were terminated and reverted back to a previous phase, implying that a decision to accept or reject an item occurred in those phases. Once the dart was initiated 96% of the attempts to capture prey were successful.

Flexibility in the sequence of phases of foraging behavior is adaptive for minimizing time and energy expenditure when feeding on food whose distribution and abundance in time and space is unpredictable. Brook stickleback foraging is consistent with optimal foraging strategies in that they (1) feed during the day, (2) feed in vegetated areas where food is most abundant and where they are protected from predators, (3) select particular taxa and size ranges within them and (4) show flexibility in foraging behavior.

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INTRODUCTION

Optimal foraging theory (Schoener 1971 , Pyke *et al.* 1977) attempts to predict foraging patterns on the basis of net energy gain per unit of time spent feeding. Alternate ways of maximizing foraging efficiency are represented by: (1) time minimizers, where time spent feeding to gather a given energy requirement is minimized and (2) energy maximizers, where excess energy gained over energy expended is maximized for a given time spent feeding.

Schoener (1971) recognized four distinct categories of optimal foraging theory by which animals can maximize their energy yield: (1) optimal diet, including selecting food of greater biomass yield per unit feeding time (LeBrasseur 1969), caloric value (Rozin and Mayer 1961), ease of handling (Brink and Dean 1966) or capture (Mech 1966, *in* Schoener 1971), (2) optimal foraging space, maximizing fitness as a function of home range size, patch selection, foraging path or movement within feeding area and exclusiveness of feeding area, (3) optimal foraging period, maximizing energy intake and minimizing metabolic costs of activity under time distributions of climatic factors and food and predator abundance and (4) optimal foraging group size, relating hunting group size to foraging efficiency, probability of predation and defendable area per unit cost of defense.

The present study is an examination of the feeding behavior of the brook stickleback, Culaea inconstans (Kirtland), and a description of its foraging behavior. The brook stickleback, distributed throughout north-central North America, is one of the most cold-adapted freshwater fish and exhibts little resistance to high temperatures, thus limiting its southern distribution and habitat (Winn 1960). Brook stickleback generally inhabit cool, clear, shallow, freshwater streams or ponds with a dense growth of aquatic vegetation (Reisman et al. 1967).

Stickleback populations are usually composed of fish in their first year (age 0) although two and three-year-old fish (age 1+) may be present (Wootton 1976). Stickleback are mainly carnivorous, their food consisting of aquatic insect larvae, crustaceans, snails, oligochaetes and eggs and larvae of fish, including their own (Scott and Crossman 1973). In turn they form the prey of predatory fish such as pike, fish-eating birds, piscivorous mammals (Wootton 1976), and certain invertebrates (Reist 1980).

This study is a description of where brook stickleback live (and feed), the time of feeding on a daily and seasonal basis, the degree to which they select certain taxa and certain sizes within particular taxa and their foraging behavior. Information on prey selectivity by Culaea has not been reported previously.

METHODS

Plan of study.

Feeding selectivity was assessed by comparing the relative proportions of food items in the fish's environment with those they consumed. Thus it is important to know when and where fish are feeding so that the fish and their potential food items are sampled at relevant times and places. Stickleback were sampled from June to August at 4h intervals over 24h from both vegetated and open water areas at three sites to determine the time and place of feeding. Analysis of food selection was then made on fish and invertebrates collected at the appropriate times and places. Consequently the extent to which stickleback optimize diet, time and space can be assessed.

Study sites.

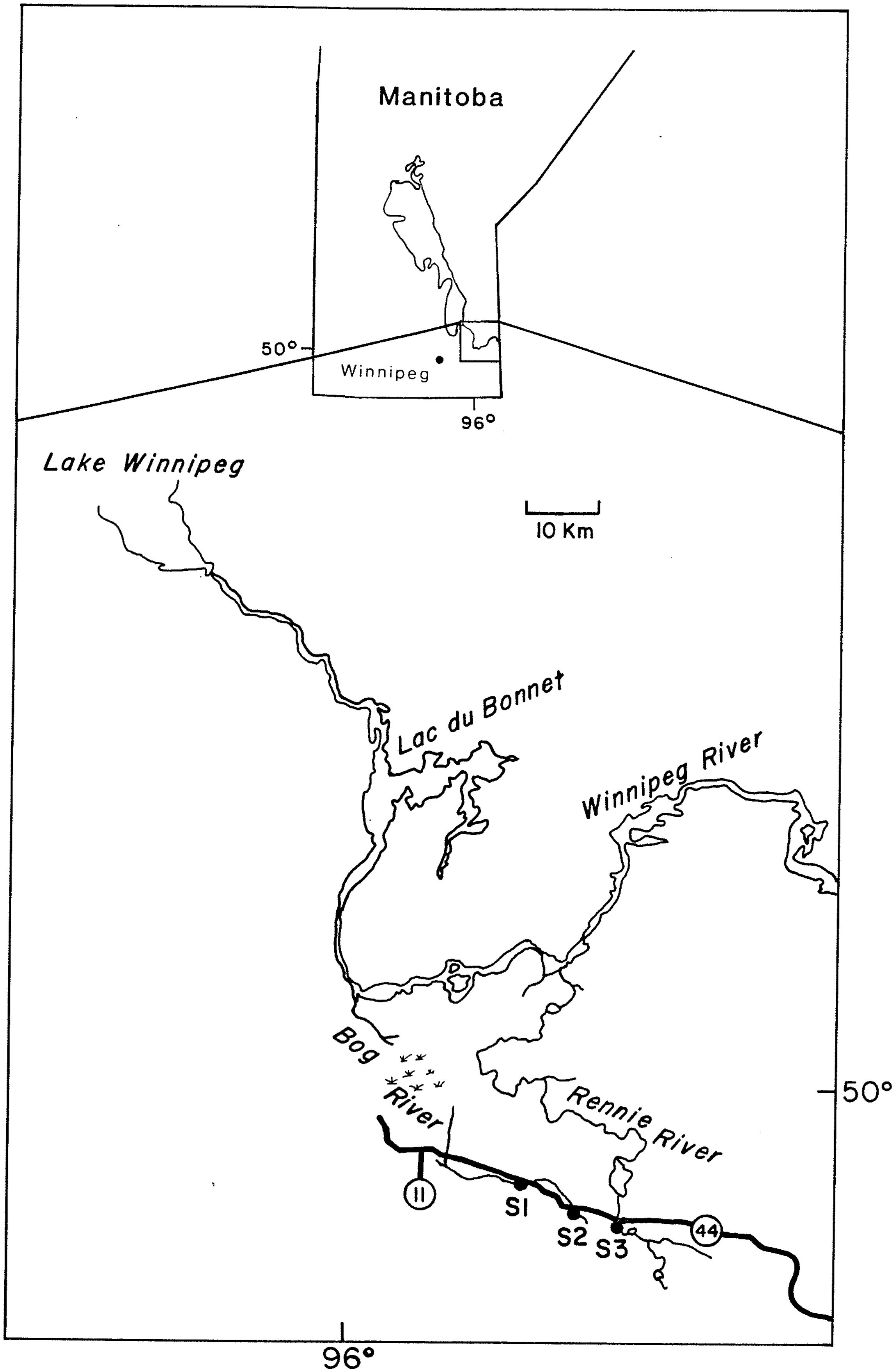
The Bog and Rennie Rivers (Winnipeg River drainage system) and the Brokenhead River, located in southeastern Manitoba were used in this study. All streams are small and meander through a combination of marshland and coniferous-deciduous forests, on the western edge of the Canadian

Shield, and drain ultimately into Lake Winnipeg. An average water velocity of $60cm \cdot sec^{-1}$ was reached in early spring during meltwater runoff and then declined to virtually 0 by late summer. Water flow under the ice was negligible.

Sites 1 and 2 (Fig. 1) were located on the Bog River. Site 1 consisted of a slow-flowing channel (<10m wide; <3m deep) and adjoining backwaters. The stream bed was composed of a sand-silt mixture with silt deposits along the banks. Overhanging vegetation was scarce and aquatic vegetation consisted of *Myriophyllum* sp., *Vallisneria* sp. and *Sparganium* sp. In addition to brook stickleback, the central mudminnow (*Umbra limi*, Kirtland), northern redbelly dace (*Chrosomus eos*, Cope), finescale dace (*Chrosomus neogaeus*, Cope), fathead minnow (*Pimephales promelas*, Rafinesque), and pearl dace (*Semotilus margarita*, Cope) were common species.

Site 2 was located in a small (<2m wide; <2m deep) channel. The substrate was composed entirely of silt. There was some overhanging vegetation, with aquatic vegetation and fish species similar to site 1.

Figure 1: Map of the Winnipeg River drainage system, Manitoba, showing study sites 1 to 3 located on the Bog and Rennie Rivers. Note: S, site, P.T.H., Provincial Trunk Highway.


Manitoba
50°
Winnipeg
96°
Lake Winnipeg
10 Km
Lac du Bonnet
Winnipeg River
Bog River
Rennie River
50°
11
S1
S2
S3
44
96°

Site 3 on the Rennie River (Fig. 1) consisted of a small (<10m wide; <3m deep) channel and still backwater pool. The stream bed was primarily sand-gravel with silt deposits along the vegetated edges. There was little overhanging vegetation and aquatic vegetation consisted of *Myriophyllum* sp., *Vallisneria* sp., *Sparganium* sp., *Nuphar* sp. and *Elodea* sp. Other fish species included the Iowa darter (*Etheostoma exile*, Girard) in addition to those listed above. Northern pike (*Esox lucius*, Linnaeus) and yellow perch (*Perca flavescens*, Mitchell) were encountered rarely.

Feeding behavior of brook stickleback was observed in a small pool (<10m wide; <1.5m deep) on a tributary of the Brokenhead River, near Richer, Manitoba. The substrate was a sand-gravel mixture with silt deposits in the vegetation. This location was heavily vegetated with *Sparganium* sp., *Elodea* sp. and *Myriophyllum* sp.

Fish collections.

To describe the qualitative and quantitative aspects of feeding biology, stickleback were collected from three sites in the stream margin environment periodically from June, 1979 to May, 1980. Throughout the ice-free period fish were collected by hauling a 2-man seine (2m X 1.4m, $2mm^2$ mesh) through the vegetated stream margins. In June, July and August, 1979 and May, 1980 fish were collected over a 24h period, every 4h starting at 0800h. In September, 1979 three collections were made at 0600, 1200 and 1600h. One series of samples was taken at 1200h in October, 1979 and April, 1980.

Fish were collected under the ice (November, 1979 to March, 1980) using plastic minnow traps (length 43cm; diameter 21cm). In December, 1979 February and March, 1980 fish were collected by setting traps under ice for 2 to 4h between 1000 and 1500h.

All fish caught were killed in a 1% phenoxyethanol solution to prevent regurgitation of stomach contents and then preserved in a 10% formalin solution.

Environments occupied by brook stickleback.

To determine the distribution and density of brook stickleback in particular environments in the Bog and Rennie Rivers, monthly collections were made from June to October, 1979 (at the same times mentioned above) in two environments: the vegetated stream margin and the relatively vegetation-free stream center. Both environments were sampled at all sites. Areas seined at any one time in the stream margins or in the stream centers ranged from 1 to $36m^2$ and 3 to $116m^2$, respectively. Densities of fish were calculated by dividing the total number of fish caught in each environment by the total area seined. To determine if the density of fish varied between environments a chi-square goodness of fit test was performed on all collections.

Diurnal and seasonal feeding periodicity.

Brook stickleback were collected at 4h intervals over one 24h period in each of June, July and August, 1979 to determine the time of feeding. Mean feeding indices were calculated for each time period at each site by dividing the wet weight ($\pm$0.001g) of the stomach contents by the total body weight X100. Variation in the feeding indices during the day was tested using a one-way ANOVA. Feeding intensities of different age classes were compared using a sign test.

Seasonal variation in amount of food eaten was investigated by calculating a one-way ANOVA on monthly feeding indices for all fish collected between 1200 and 1600h, from June, 1979 to May, 1980. The proportion of fish with empty stomachs collected in winter was compared to non-winter samples using a 2X2 contingency table.

Diet.

To describe the proportions of different food items in the diet and their seasonal variation, stomach contents were examined from at least 10 stickleback (5 adult and 5 young of the year where possible) selected randomly from each sample collected between 0800 and 2000h, at each site from June, 1979 to May, 1980. Fish weight ($\pm$0.001g) and standard length ($\pm$0.01mm) were recorded. Two age groups, young of the year (0) and adults (1+), were distinguished by length frequency distributions using probability paper (Cassie 1954, Appendix 1). Stomach contents were removed, identified and enumerated. The proportion of each food item in the diet each month was calculated for age 0 and 1+ fish from each site.

Relative abundance of food items in the diet were described using percent composition by number . Numerical analysis is inadequate only when a significant component of the diet does not occur in discrete units (e.g. filamentous algae and detritus; Windell and Bowen in Bagenal 1978). As these items were rare in the diet and since stickleback do not chew their food, food items remain intact, facilitating identification and enumeration.

Abundance of prey in the environment.

The abundance of prey in the environment occupied by the fish at times when the fish were feeding was determined by sampling invertebrates simultaneously at places adjacent to those where fish were collected for stomach analysis. Plankton samples were collected by oblique tows with a 80μm mesh plankton net mounted on a 60cm handle. Oblique tows were representative of all depth strata and the volume of water sampled ranged from 23.4 to 140.4L. Samples were preserved in a 70% isopropyl alcohol solution and Rose

Bengal added in a concentration of $0.4g \cdot L^{-1}$, to increase visual contrast between the organisms and detritus. Samples sat for at least 48h before processing to allow the stain to take effect.

Plankton samples were rinsed in a 50µm mesh plankton sieve and concentrated to fixed volumes (range 55-500ml). Subsamples were obtained using a Nalgene variable volume dispenser (model 3702). The subsampler consisted of a 500ml transparent polyethylene wash bottle with an attached measured chamber, graduated from 1 to 25ml. When the bottle is squeezed liquid is forced into the chamber. On releasing the pressure the excess liquid returns to the bottle and the measured amount can be poured.

The contents of the bottle were shaken vigorously prior to each subsample and at least four, 1ml subsamples were taken. Edmondson et al. (1971) recommended counting at least 40 individuals of the major species to represent adequately the population. Sufficient subsamples were processed to achieve this number. To evaluate the accuracy of the subsampling method a variance to mean ratio test (Cassie in Edmondson et al. 1971), was performed on the subsamples of three plankton samples (Appendix 2). All planktonic organisms were identified and enumerated, and densities determined by dividing the number$\cdot L^{-1}$ by the total volume of water sampled.

Invertebrate taxa were identified to family for Cladocera (Birge _in_ Ward and Whipple 1959) and Diptera (Teskey _in_ Merritt and Cummins 1978) order for other Insecta and Arachnida, suborder for Copepoda and class or subclass for the remainder (Pennak 1953). The percent composition of the samples was determined by dividing the number of each organism$\cdot L^{-1}$ by the total number of organisms$\cdot L^{-1}$ X100.

<u>Prey selectivity by brook stickleback.</u>

To determine if brook stickleback fed selectively, the relative proportions of food organisms in the diet and in samples from the environment were compared using a modification of Ivlev's electivity index (1961). The formula for determining electivity is

$$E = (r_i - p_i)/(r_i + p_i)$$

where:

E = the electivity index

r_i = the percent of item i in the diet

p_i = the percent of item i in the environment

Electivity values were calculated for only those items that had a percent composition >3.5% in either the diet or the environment samples. Values obtained by this method can range from -1 (avoidance) to +1 (selection). Absence of selection was arbitrarily set at electivity values between -.20 and +.20 inclusive, negative selection by electivity values less than -.20 and positive selection by electivity values greater than +.20.

Size selectivity.

To investigate selectivity for food size by age 0 and 1+ stickleback, size frequency distributions of chironomid larvae and Chydoridae in the stomach contents were compared to those in the environment samples. At least 40 individuals of each taxon were randomly selected both from the stomachs of each age class and from the environment samples each month. Chironomid larvae used were obtained from 1200h samples taken during July, August and September, 1979. Chydorids used were obtained from 1200 and 1600h samples taken from June to September, 1979.

Measurements of the maximum width or maximum dorso-ventral depth, whichever was greater, were taken. Chironomids and chydorids were measured using a dissecting microscope, fitted with an 80X occular micrometer. Organisms larger than 1.5mm were measured using calipers. Chironomid larvae and chydorids were separated into seven size classes, each 0.05mm, from 0 to .31+mm for the former and from .10 to .40+mm for the latter.

To test whether the size frequency distributions differed, a 2XC contingency table was used. Chi-square values $\leq p = 0.05$ indicated that the frequency distributions differed significantly from each other by more than random sampling error.

Maximum mouth diameter was measured ($\pm$0.13mm) by inserting a tapered cyclindrical steel probe calibrated in increments of 0.34mm. The relationship between size of stickleback and the maximum diameter of prey that can be ingested was determined by a linear regression analysis of ln mouth diameter on ln standard length ($\pm$0.01mm) performed on 178 fish selected randomly from site 3 from July to September, 1979.

Foraging behavior.

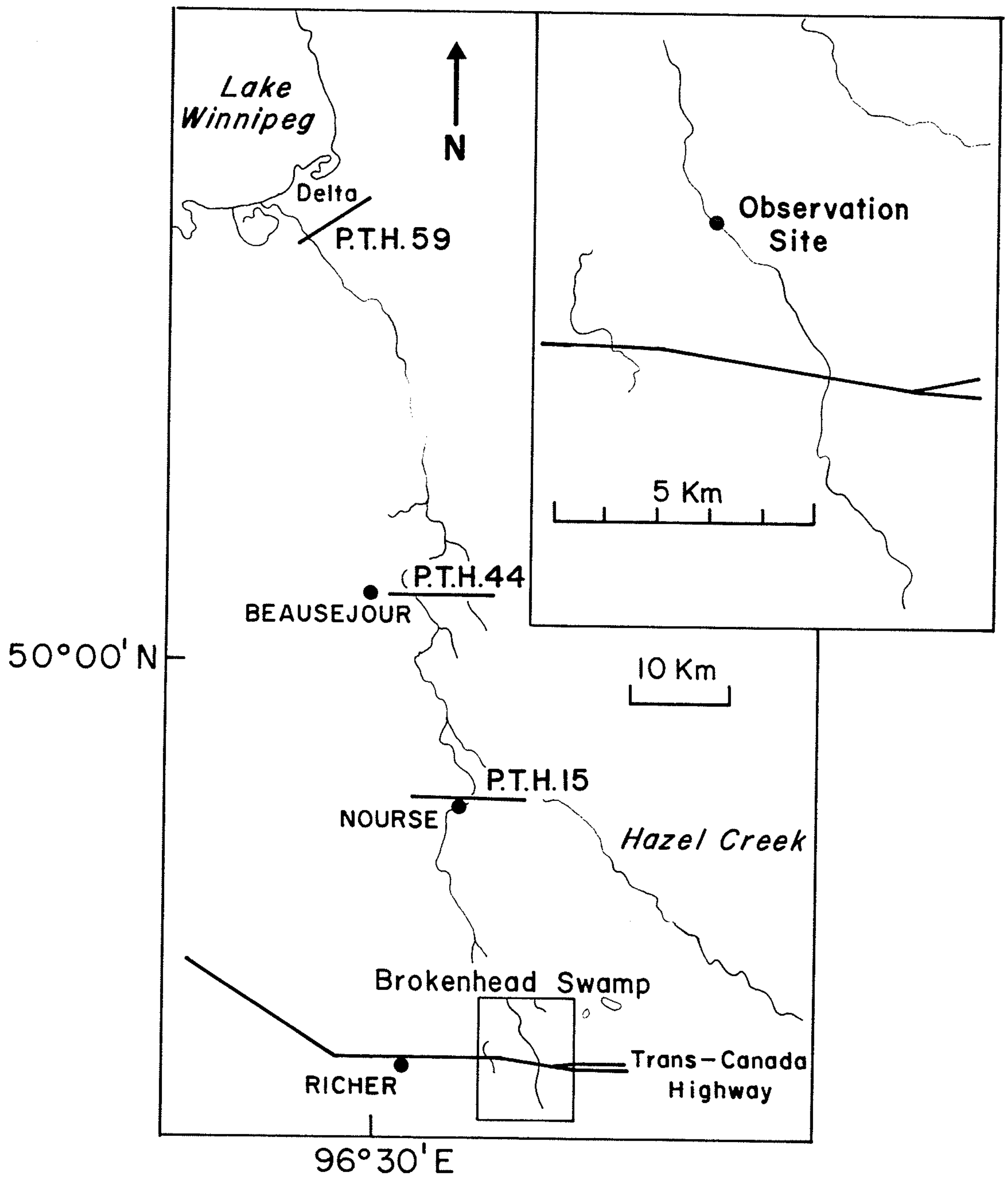
To investigate the feeding behavior of stickleback in the field, fish were observed in a tributary of the Brokenhead River, near Richer, Manitoba (Fig.2). Observations were made on 30 August, 1979, 10 July, 1980 and 23 July, 1980 using a wetsuit, faceplate and snorkel.

The feeding behavior of the stickleback can be described as a sequence of five phases forming three responses. The searching response consists of a swimming phase followed by a hovering phase in which the fish remains motionless in a horizontal position within 30cm of the bottom, and scans the substrate or vegetation for prey. The pursuit response refers to the time from detection of prey to the time contact is made or until the fish reverts back to searching. The first sighting of prey is represented by commencement of the aiming phase in which the fish tilts, head downward, from the horizontal position by about 45 degrees while approaching the substrate (to within 10-15cm) and fixates the prey. If the prey is appropriate (i.e. in size, palatability, etc.) the aiming phase is followed by a short, rapid dart at the food item. This phase is so rapid its time was difficult to measure in the field and was assumed to be equal to one second.

The consummatory response consists of the handling phase representing time required to seize, manipulate and swallow the prey. Sticklebacks do not chew their food and no swallowing movements were evident, therefore the handling phase was assumed to last until the start of any of the preceeding phases. A darting phase followed by another dart was assumed to represent failure in seizing or swallowing the prey item.

Fish were observed between 1000 and 1500h, to coincide with observed time of maximum feeding activity. It was assumed in these observations that the fish were continuously foraging. Fish were observed in the sparsely vegetated stream center and along the margins of the vegetated stream edges.

Figure 2: Map of the Brokenhead River drainage system showing observation site. Note: P.T.H., Provincial Trunk Highway.


Lake
Winnipeg
N
Delta
P.T.H. 59
Observation
Site
5 Km
P.T.H.44
BEAUSEJOUR
50°00' N
10 Km
P.T.H. 15
NOURSE
Hazel Creek
Brokenhead Swamp
Trans-Canada
Highway
RICHER
96°30' E

Fifty-five fish were observed individually over 5 min intervals and the sequence and time of each phase were recorded. Mean time spent in each phase when that event occurred and standard deviations of the mean, percent time spent in each phase and frequencies of each phase sequence were calculated to ascertain how stickleback partitioned time during feeding activities. To determine the position in the environment where the stickleback forage the number of darts individual fish made over 5 min intervals was calculated for 3 locations: bottom substrate, vegetation and water column.

RESULTS

Environments occupied by the brook stickleback.

Densities of fish in the margin and center environments were significantly different ($p<0.005$). Brook stickleback were consistently more abundant in the vegetated stream margins than in the stream centers (Table 1). Densities of fish in the stream centers were generally low, ranging from 0-7.6 fish$\cdot m^{-2}$ as compared to 6.8-29.0 fish$\cdot m^{-2}$ in the stream margins.

Diurnal and seasonal feeding periodicity.

Feeding intensity of stickleback varied significantly during the day ($p=0.0001$). Feeding by brook stickleback began at dawn, continued throughout the day, and ceased at sunset (Table 2). There was little feeding at night. Feeding indices reached a maximum between 1200 and 2000h, and a minimum at 0400h. Of 340 fish analysed from the 2400h to 0400h samples, 37% had empty stomachs compared to 1% of 600 fish from the 0800 to 2000h samples. When present age 0 fish generally had a greater feeding index than age 1+ fish ($p<0.005$; Appendix 3).

Table 1. Density (number·m^{-2}) of stickleback in two environments with area (m^2) seined in parentheses.

Month	Environment	Site 1	Site 2	Site 3
June	Margin	9.0 (28)	6.9 (16)	11.9 (11)
	Center	0.3 (116)	0.6 (41)	7.6 (31)
July	Margin	21.7 (21)	19.7 (27)	11.6 (16)
	Center	3.9 (58)	3.1 (27)	0.2 (82)
August	Margin	8.5 (36)	15.7 (12)	11.0 (15)
	Center	0.5 (55)	5.9 (25)	0.1 (60)
September	Margin	6.8 (8)	23.3 (3)	9.0 (7)
	Center	0.3 (24)	3.3 (11)	0 (24)
October	Margin	10.0 (2)	29.0 (1)	7.3 (6)
	Center	0 (3)	5.3 (3)	- -

Table 2. Feeding indices of age 0 and 1+ stickleback by month (average of 3 sites).

Month	Age	Time of day (h)					
		0400	0800*	1200	1600	2000	2400
April	1+			1.0			
May	1+		1.3	1.3	1.2	2.5	
June	1+	0.3	1.0	1.7	1.8	1.4	0.8
July	0	0.5	1.6	1.6	1.9	2.0	1.5
	1+	0.1	0.7	0.8	1.0	1.0	0.7
August	0	0.2	1.0	1.6	1.6	1.8	1.0
	1+	0.1	0.6	1.1	1.2	1.1	0.5
September	0		0.3	1.1	1.1		
	1+		0.3	1.0	1.4		
October	0			1.1			
	1+			0.6			
Mean		0.3	0.9	1.2	1.4	1.7	0.9

Note: * , In September fish were collected at 0600 h.

There was substantial seasonal variation in the amount of food eaten (p=0.0001; Table 3). A significant amount of food was present in the stomachs in April (mean of 1.0) increasing to a seasonal maximum in June (mean of 1.8). The amount of food in the stomachs decreased progressively through the remainder of the year and reached a minimum feeding index of 0.1 in winter (December, February and March). Of the fish collected in winter 60% had empty stomachs compared to 1.3% of fish collected during the remainder of the year ($p<0.005$).

Diet.

Brook stickleback were predominantly carnivorous, eating a wide variety of planktonic and benthic organisms. The number of prey consumed per fish varied considerably among sampling dates and sites (Appendix 4). They consumed crustaceans, annelids, arachnids, molluscs, insect larvae and fish eggs and larvae. Most of the diet was animal in origin although they did consume small amounts of algae and detritus.

In April, Cyclopoida and chironomid larvae were most frequently eaten while in May these and simuliid larvae were predominant in the diet (Table 4). Chydorids and ostracods were most numerous in June while in July, August, September and October Chydoridae, chironomid larvae, Sididae (August) and Cyclopoida (October) were most frequently consumed.

Table 3. Seasonal variation in mean feeding indices of stickleback collected at 1200 and 1600 h for all 3 sites. (Winter - December, 1979 and February and March, 1980).

	Apr.	May	June	July	Aug.	Sept.	Oct.	Winter
Feeding Index	1.0	1.3	1.8	1.3	1.3	1.0	0.7	0.1
n	30	52	130	83	79	110	60	51

Table 4. Percent composition of stomach contents of age 0 and 1+ stickleback by month (values represent means of 1-4 replicates at each of 3 sites; winter values based on 51 fish collected from sites 1 and 2 during December, February and March).

Food Category	April	May	June	July		August		September		October		Winter
	1+	1+	1+	0	1+	0	1+	0	1+	0	1+	1+
Cyclopoida	41.2	22.9	13.4	10.7	7.4	11.3	7.7	14.3	11.3	13.3	29.4	34.7
Harpacticoida	7.0	2.4	16.8	0.3	0.3	0.1	0.1	0.1	0.2	0.6	7.5	-
Chydoridae	-	8.8	23.8	23.4	41.5	25.1	25.6	44.2	42.1	39.2	27.6	7.7
Sididae	0.2	0.5	0.3	2.6	0.9	24.0	6.2	3.2	3.7	-	0.5	-
Bosminidae	-	-	4.0	10.9	4.0	9.6	10.8	2.0	1.6	1.7	0.4	-
Daphnidae	-	0.5	0.1	2.0	0.3	0.8	0.8	1.6	2.1	0.2	0.7	-
Ostracoda	0.5	8.0	20.8	7.1	4.7	5.9	4.5	7.2	4.7	0.5	1.1	2.9
Chironomidae l.	38.1	31.0	12.1	29.2	36.2	19.8	35.8	22.7	26.8	36.9	26.1	54.7
Simuliidae l.	-	18.3	0.8	-	-	-	-	-	-	-	-	-
Other	13.0	7.6	7.9	13.8	4.7	3.4	8.5	4.7	7.5	7.6	7.4	-
n	3	12	12	12	12	12	12	12	9	9	3	3

Note: l., larvae

During winter, cyclopoids and chironomids appeared most frequently in the diet. No consistent differences between ages 0 and 1+ were evident (Appendix 5).

Abundance of prey in the environment.

The abundance of food organisms in the environment varied substantially over the year at all sites (Appendices 6 and 7). The total density of organisms increased from a minimum of $11.2 \cdot L^{-1}$ in April to a maximum of $167.5 \cdot L^{-1}$ in August, about 15 times greater (Table 5). Prey density decreased from August to October but remained greater than that of April. Estimates of prey abundance during the winter months were not made although Ostracoda, Cyclopoida, chironomid larvae and other insect larvae were collected then in Ekman samples.

Of the dominant invertebrates in the environment samples (Table 6), Cyclopoida, Chydoridae, Ostracoda, and chironomid larvae were present during all months. Cyclopoida and naupli (other, in Table 6) were the most abundant organisms in April and May. Cyclopoida and Chydoridae were most frequently collected from June to October, 1979 although chironomid larvae were present in significant proportions. The remaining invertebrates were considerably less common, constituting on the average, 11% of the total food items.

Table 5. Seasonal variation in the mean total density (number·L^{-1}) of all food items in the environment.

	April	May	June	July	Aug.	Sept.	Oct.
Density	11.2	59.3	80.7	137.7	167.5	148.2	40.4

Table 6. Percentage composition (by number) of food items in the environment by month (values represent mean of 1-4 replicates at each of 3 sites).

Food Category	Apr.	May	June	July	Aug.	Sept.	Oct.
Cyclopoida	11.0	39.9	27.5	23.6	29.6	27.9	34.6
Harpacticoida	9.3	2.0	1.1	0.1	0.2	-	2.2
Chydoridae	1.8	9.6	37.0	20.3	27.4	34.1	31.5
Sididae	-	0.4	0.3	2.0	8.3	1.3	-
Bosminidae	-	0.1	1.1	5.8	0.6	0.2	-
Daphnidae	-	-	1.3	3.6	1.9	0.4	0.2
Ostracoda	3.3	11.2	14.1	11.2	5.0	2.4	4.0
Chironomidae l.	4.8	9.1	17.7	15.2	18.4	27.9	17.6
Simuliidae l.	1.5	4.5	0.3	0.1	-	-	-
Other	68.3	22.1	8.7	18.1	8.5	5.6	9.7
n	3	12	12	12	12	9	3

Note: l., larvae

Prey selectivity by brook stickleback.

Mean electivity values for the nine most common items in the diet of the brook stickleback in this study indicate selectivity by Culaea for particular prey items (Tables 7 and 8). Of the Copepoda, Cyclopoida were generally negatively selected or consumed in a proportion similar to that in the environment samples while Harpacticoida when present were usually positively selected. Chironomid larvae were, with few exceptions either positively selected or selected in a similar proportion as they occured in the environment samples. The four families of cladocerans were selected to various degrees . Chydorids were generally avoided or eaten as encountered from April to August but positively selected or selected in a proportion similar to that of the environment samples in September and October. Sididae and Bosminidae were always positively selected or selected in a similar proportion as they occur in the environment samples. Ostracoda showed no consistent trends of selection or rejection. Daphnidae and Simuliidae were too infrequent in the diet for any generalities to be made. Electivities of age 0 and 1+ fish were generally similar (Table 7).

Table 7. Monthly electivity indices for the nine most important food items of the brook stickleback by site. Where missing values occur, the % composition of that item in the stomach and the environment was < 3.5%. Values based on at least 3 replicates except April and October.

Food Category	April	May	June	July		August		September		October	
	1+	1+	1+	0	1+	0	1+	0	1+	0	1+
1.											
Cyclopoida	+.58	-.07	-.30	-.09	-.14	-.42	-.44	+.95	+.93	-.25	-.20
Harpacticoida	+1.00		+.59								+.59
Chydoridae	-1.00	+.01	-.33	-.44	-.26	-.32	-.52	+.99	+.98	+.37	+.01
Sididae				+.30	+.14	+.49	-.11	-.05	-.13		
Bosminidae						+.76	+.92	+1.00	+1.00		
Daphnidae								-.24	-.16		
Ostracoda	-.49	-.10	+.13	+.07	0	-.48	-.21	+.18	+.53	-.86	-.81
Chironomidae l.	+.27	+.48	+.45	+.31	+.35	+.05	+.27	-.34	-.19	+.05	+.59
Simuliidae l.		+.66									
2.											
Cyclopoida	+1.00	-.51	0	-.70	-.60	-.50	-.53	-.03	-.09	-.07	-.04
Harpacticoida	+1.00		+.76							-.20	-.41
Chydoridae	-1.00	-.52	-.28	+.07	-.30	+.10	-.06	+.15	+.14		+.01
Sididae									+.30	-.16	
Bosminidae				+.38							
Daphnidae											
Ostracoda		-.91	+.28	-.29	-.29	-.08	+.08	-.68	-.16		
Chironomidae l.	-.24	+.43	-.18	-.03	+.05	-.09	+.22	-.26	-.35	+.14	+.03
Simuliidae l.	-1.00	+.27									
3.											
Cyclopoida	+.21	-.39	-.34	-.39	-.62	-.48	-.65	-.63	-.70	-.45	+.01
Harpacticoida	-.41	+.47									
Chydoridae		+.34	-.01	-.33	-.48	-.13	-.15	+.32	+.21	-.09	-.33
Sididae				+.19		+.31	-.01				
Bosminidae			+.90	+.31	+.06	+.94	+.81				
Daphnidae				-.08	-.84						
Ostracoda		+.31	+.31			+.52	+.11	+.77	+.72		
Chironomidae l.	+1.00	+.63	-.02	+.49	+.62	+.10	+.43	+.16	+.40	+.25	+.27
Simuliidae l.											

Note: l., larvae

Table 8. Selectivity (by month) for the nine most important food items of the brook stickleback. Where missing values occur, the % composition of that item in the stomach contents or the environment was < 3.5%. Values based on at least 3 replicates except April and October.

Food Category	April	May	June	July		August		September		October	
	1+	1+	1+	0	1+	0	1+	0	1+	0	1+
1											
Cyclopoida	+	0	–	0	0	–	–	+	+	–	0
Harpacticoida	+		+								+
Chydoridae	–	0	–	–	–	–	–	+	+	+	0
Sididae				+	0	+	0	0	0		
Bosminidae						+	+	+	+		
Daphnidae								–	0		
Ostracoda	–	0	+	0	0	–	–	0	+	–	–
Chironomidae l.	+	+	+	+	+	0	+	–	0	0	+
Simuliidae l.		+									
2											
Cyclopoida	+	–	0	–	–	–	–	0	0	0	0
Harpacticoida	+		+							0	–
Chydoridae	–	–	–	0	–	0	0	0	0		0
Sididae									+	0	
Bosminidae				+							
Daphnidae											
Ostracoda		–	+	–	–	0	0	–	0		
Chironomidae l.	–	+	0	0	0	0	+	–	–	0	0
Simuliidae l.	–	+									
3											
Cyclopoida	+	–	–	–	–	–	–	–	–	–	0
Harpacticoida	–	+									
Chydoridae		+	0	–	–	0	0	+	+	0	–
Sididae				0		+	0				
Bosminidae			+	+	0	+	+				
Daphnidae				0	–						
Ostracoda		+	+			+	0	+	+		
Chironomidae l.	+	+	0	+	+	0	+	0	+	+	+
Simuliidae l.											

Note: – , mean electivity between $^{-}.20$ and $^{-}1.00$

\+ , mean electivity between $^{+}.20$ and $^{+}1.00$

0 , mean electivity between $^{-}.20$ and $^{+}.20$

l , larvae

Size selectivity.

Size frequency distributions of chironomid larvae consumed by age 0 and 1+ fish were similar for July, August and September but differed significantly from those present in the environment (Table 9). Smaller size classes were more frequent in the stomachs than in the environment.

Chydorids consumed by age 0 fish, at all times, were significantly different from the size frequency distributions consumed by age 1+ fish or those present in the environment samples. Smaller size classes of chydorids were more frequent in the diet of age 0 fish. The size frequency distribution of chydorids in the diet of age 1+ fish was similar to that in the environment samples in July and September but differed in June and August (Table 10).

The linear regression analysis of ln mouth diameter on ln standard length was highly significant, $p=0.001$ and $R^2=0.99$. The relationship of mouth diameter to standard length can be expressed by the equation

$$y = 0.06\ (X^{1.01})$$

Thus for any value of standard length X the corresponding mouth diameter Y can be estimated. The mean mouth diameter of age 0 fish ranged from 1.3mm in July to 1.9mm in September. The mean mouth diameter of age 1+ fish ranged from 2.1mm in June to 2.7mm in September. Consequently,

Table 9. Size class frequency distributions and median sizes of Chironomidae larvae in the environment and stomach contents of age 0 and 1+ fish, and range of fish mouth diameter by age class, from July to September.

	Σ	Size Class Mean (mm)									Median Size (mm)	Range Mouth Diameter (mm)
		.075	.125	.175	.225	.275	.325	.375	.425			
July												
Environment	45	1	4	6	9	9	3	4	9	] *	.27	
Age 1+	40	2	7	21	5	5	–	–	–	] *	.19	1.8 - 3.0
Age 0	40	–	13	20	7	–	–	–	–	] n.s.	.18	0.7 - 1.8
August												
Environment	45	2	3	10	10	7	5	2	6	] *	.24	
Age 1+	45	3	11	13	10	8	–	–	–	] *	.19	2.1 - 3.0
Age 0	40	5	13	12	5	5	–	–	–	] n.s.	.17	0.8 - 2.1
September												
Environment	45	1	2	14	12	8	3	2	3	] *	.23	
Age 1+	42	4	9	9	6	14	–	–	–	] *	.20	2.4 - 3.3
Age 0	40	6	8	13	4	9	–	–	–	] n.s.	.18	1.3 - 2.4

Note: Σ - number of observations; n.s. - not significant, * - significant ($p < 0.05$)

Table 10. Size class frequency distributions and median sizes of Chydoridae in the environment and stomach contents of age 0 and 1+ fish, and range of fish mouth diameter by age class from June to September.

	$\sum$	Size Class Mean (mm) .12	.17	.22	.27	.32	.37	.42		Median Size (mm)	Range Mouth Diameter (mm)
June											
Environment	50	-	2	14	12	18	3	1	] * (Environment–Age 1+)	.29	
Age 1+	50	-	2	18	7	16	7	10		.33	1.5 - 3.3
Age 0				not present							
July											
Environment	50	1	5	21	19	4	-	-	] n.s. (Environment–Age 1+)	.25	
Age 1+	60	4	9	28	10	8	1	-	] * (Age 1+–Age 0);] * (Environment–Age 0)	.22	1.8 - 3.0
Age 0	40	3	19	13	4	1	-	-		.19	0.7 - 1.8
August											
Environment	50	-	5	24	19	-	2	-	] * (Environment–Age 1+)	.24	
Age 1+	50	1	13	18	10	7	1	-	] * (Age 1+–Age 0);] * (Environment–Age 0)	.23	2.1 - 3.0
Age 0	50	-	14	19	5	1	1	-		.21	0.8 - 2.1
September											
Environment	50	-	7	19	20	3	1	-	] n.s. (Environment–Age 1+)	.25	
Age 1+	50	-	10	21	14	3	2	-	] * (Age 1+–Age 0);] * (Environment–Age 0)	.24	2.4 - 3.3
Age 0	50	-	22	20	7	-	1	-		.21	1.3 - 2.4

Note: $\sum$ - number of observations; n.s. - not significant; * - significant ($p < 0.05$)

both adult and young of the year fish were capable of ingesting all size classes of chydorids and chironomids present in the environment (Tables 9 and 10).

Foraging behavior.

Stickleback were observed to feed more frequently on prey items from the substrate (78% of the feeding bites) than on the vegetation or in the water column (Table 11). The sequence of feeding phases was not fixed; the occurrence of all five phases in succession was uncommon (Table 12). The dart was not necessarily preceeded by all other phases nor were all sequences completed. The searching response was not included in 32.8% of the feeding patterns. Of the feeding sequences that included the swimming phase 34% were followed by the hover phase, 60.5% omitted the hover phase and went directly to the aim phase and a small proportion went straight to the dart phase (Figure 3). Of the feeding sequences that included hover, 47.9% were terminated (reverted to a preceeding phase) in this phase. Of the feeding sequences that included aiming, 40.4% terminated in this phase. Once the fish reached the dart phase, 96% of the attempts to capture prey were successful.

When they occurred, the swim, hover and aim phases were of similar duration (7.9-9.4 sec), considerably longer than the time for the dart or handling phase (Table 13). Although the aim phase accounted for the greatest porportion

Table 11. Frequency of bites over 5 min intervals in 3 locations. Percent in parentheses.

Location Of Bite	Mean number of bites · 5 min $^{-1}$		Standard Deviation	Standard Error	Range
Bottom	8.5	(78)	7.0	1.1	0 - 27
Vegetation	2.1	(19)	4.2	0.7	0 - 18
Water column	0.3	(3)	0.7	0.1	0 - 3

Table 12. Frequency and % occurrence of phase sequences exhibited by brook stickleback while foraging. Values based on observations of 55 fish for 5 min intervals.

PHASE SEQUENCE	FREQUENCY	% OCCURRENCE
S H A D h	28	2.8
S _ A D h	176	17.3
S H A D _	6	0.6
S H _ D h	15	14.7
S _ _ D h	26	2.6
S _ _ D _	3	0.3
S H A _ _	32	3.1
S H _ _ _	102	10.0
S _ A _ _	134	13.2
_ H A D h	46	4.5
_ H _ D h	16	1.6
_ H _ D _	2	0.2
_ H _ A _	37	3.6
_ H _ _ _	60	5.9
_ _ A D h	143	14.1
_ _ A D _	8	0.8
_ _ A _ _	73	7.2
_ _ _ D h	106	10.4
_ _ _ D _	4	0.4

Note: S - swim; H - hover; A - aim; D - dart; h - handle

Figure 3: Percent of feeding sequences selected at each feeding phase. Note: A - sequences including swim, B - sequences including hover, C - sequences including aim.

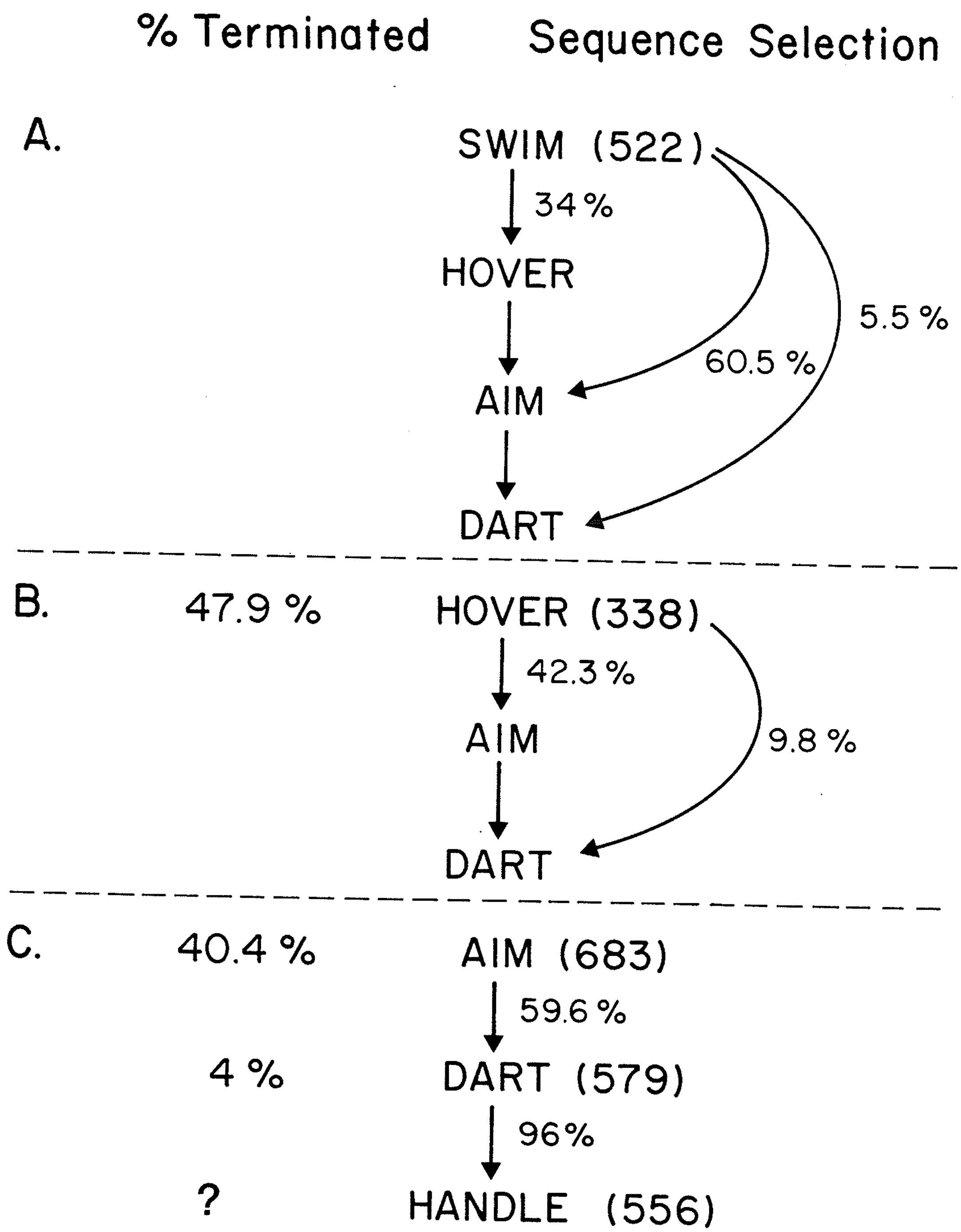

% Terminated
Sequence Selection
A.
SWIM (522)
34 %
HOVER
60.5 %
5.5 %
AIM
DART
B.
47.9 %
HOVER (338)
42.3 %
9.8 %
AIM
DART
C.
40.4 %
AIM (683)
59.6 %
4 %
DART (579)
96%
?
HANDLE (556)

Table 13. Mean time (sec) per feeding phase when that event occurred.

Phase	Mean time per phase (sec)	S. D.	Range of mean time	95% C.I.M.	n
Swim	8.5	8.7	1 - 79	7.7 - 9.3	522
Hover	9.4	12.5	1 - 157	8.0 - 10.8	338
Aim	7.9	7.9	1 - 55	7.3 - 8.5	683
Dart	1.0	0	0		579
Handle	4.8	3.1	1 - 19	4.5 - 5.1	556

Note: S. D., standard deviation

C.I.M., confidence interval of the mean

n , number of observations

of the foraging activity the stickleback spent the greatest amount of time searching for prey (Table 14).

Table 14. Mean % time of foraging activity spent in each feeding phase, based on observations of 55 fish for 5 min intervals.

Response	Phase	Mean % Time	S. D.	Range % Time	95% C.I.M.
Search	Swim	27.3	15.8	0.7 - 72.7	23.1 - 31.4
	Hover	18.2	16.2	0 - 81.9	13.9 - 22.5
Pursuit	Aim	33.9	17.5	0 - 68.5	29.3 - 38.5
	Dart	3.7	2.2	0 - 9.1	3.1 - 4.3
Consummatory	Handle	17.0	10.3	0 - 43.0	14.3 - 19.7

Note: S. D., standard deviation

C.I.M., confidence interval of the mean

DISCUSSION

Feeding behavior of brook stickleback is in large part consistent with optimal foraging theory in three categories: optimal foraging space, optimal foraging period, and optimal diet. The stickleback's pattern of choice of food and time of feeding is such that the net rate of energy intake is maximized while time is minimized.

Optimal foraging space.

Although occurring in both the stream margin and the stream center, brook stickleback were generally confined to the stream margin environment. Although quantitative estimates of prey densities in the center environments were not determined, it is possible that fish may be concentrated in the vegetated margins due to a greater abundance of food. Hynes (1970) reports that the presence of vegetation greatly affects the fauna, with more animals present in moss, rooted plants and filamentous algae than there are in open water. Schoener (1968) suggested that available food is proportional to the area transversed and that the feeder occupies an area just large enough to supply its energy requirements. By foraging in an area of greater food abundance, stickleback minimize travelling time and energy expenditure and can afford to be prey selective. Aquatic vegetation may be necessary for other reasons; to supply nest sites and nest building materials, and to provide shelter from water currents and predators (Reisman *et al*., 1967).

Optimal foraging period.

The visually dependent components of feeding behavior (hover, aim, and dart) imply that stickleback rely predominantly on vision when searching for food. It is therefore most efficient for them to forage in daylight hours. Diurnal feeding periodicities confirm that *Culaea*, like *Gasterosteus aculeatus*, Linnaeus (Wootton 1976), fed mainly during daylight hours. Several authors, including Keast and Welsh (1968) and Elliott (1970) have found that the feeding intensity of a number of fish species varied over the diurnal cycle. According to Blaxter (1970), with few exceptions a light intensity of 10^{-1} mc (meter-candle), corresponding to late dusk, is the lower threshold for effective visual location of food by fishes. Feeding intensity of stickleback peaked between 1200 and 2000h, considerably earlier than that reported by Keast (1968) for *Culaea* in winter. The greater amount of food per g body weight consumed by age 0 fish as compared to age 1+ fish is prevalent among fish (Keast 1970 and Brett 1971) and many other animals (Schoener 1971). During their first year age

0 fish grow rapidly and have greater energy and protein demands than mature fish (LeBrasseur 1969 and Schoener 1971).

Variation in seasonal feeding intensity with considerable reduction in the amount of food consumed in winter has been observed previously in brook trout (Salvelinus fontinalis, Allan 1981) and brook stickleback (77% empty stomachs at 4C, Keast 1968). It is not known whether the observed reduction in feeding intensity in winter is due to a decline in the abundance of food organisms or to reduced metabolism of the fish as a result of low temperatures, or both (Johnson 1966 and Keast 1968).

Although the greatest abundance of food organisms in the environment occurred in August, the feeding intensity of stickleback was greatest in June. This discordance possibly resulted from efforts of post-spawning stickleback to replenish energy reserves exhausted during spawning (Hynes 1950) and coincides with the period of maximum daylight hours.

Optimal diet.

Prey types eaten were constant throughout the year with one exception. In May, stickleback fed opportunistically on large numbers of simuliid larvae which were present only at that time. Keast (1968) also reported Culaea feeding on pre-emergent simuliid larvae in April in Ontario.

Selectivity. Brook stickleback selected particular food items. Selection was strongest for sidids, bosminids, and chironomid larvae, and discontinuous for chydorids and ostracods. Cyclopoids were negatively selected, which may account for their abundance in the environment.

Large negative or positive electivity values do not necessarily mean complete avoidance or selection of an item. Most prey organisms were eaten to some extent when present in the environment. A predator may only need a small amount of an abundant item to meet its dietary requirements. Although usage is small, a conclusion that the component is of little value may not be valid. Often conclusions about selectivity are critically dependent on the array of components the investigator believes available to the animal (Johnson 1980). Caution must be exercised when interpreting usage-availability data.

Optimal foraging models (Schoener 1971 and Pyke et al. 1977) predict that the lower the absolute abundance of food or the greater the energy requirements, the greater the range of items that should be taken. Secondly, prey sizes should decrease with predator size. Finally, distributions of prey sizes eaten by a predator from a uniform distribution of size classes of prey should be larger if the predator pursues its prey over a greater distance or is relatively large than if the predator pursues its prey less or is relatively small.

Patterns of selective exploitation are a consequence of a large number of interacting predator and prey characteristics. Since stickleback are visual predators, selective predation should rely on the integration of visual acuity with morphological limitations, physiological factors, and prey availability and accessibility.

Stickleback selected particular size classes of chydorids and chironomid larvae. Smaller size classes of chydorids occurred more frequently in the diet of age 0 fish, consistent with the predictions of optimal foraging theory; food sizes decrease with decreasing predator size. Smaller size classes of chironomids were more frequent in the diet of both age classes than in the environment samples, although both age classes were morphologically capable of consuming all size ranges of chironomids and chydorids sampled from the environment. The reason for consumption of less than maximum prey size by stickleback may be due to the handling time required. Stickleback may be minimizing handling time by eating prey that are easily ingested, or alternatively, they may not be foraging optimally. Further research is required to test these alternatives.

Prey size is usually a dominant factor influencing the selectivity of visual planktivores with such size selective predation usually falling most heavily on the largest zooplankters (Brooks and Dodson 1965, Galbraith 1967, and Wong and Ward 1972). Keast and Webb (1966), Burko (1975, <u>in</u>

Hyatt 1979, with three-spined stickleback), and Hartman (1958, with rainbow trout, Salmo gairdneri) observed the size of prey consumed to be less than that for which the fish were capable of handling. A drawback to many of the foraging models is that ecologists have not considered factors other than prey size to explain selection. Size of prey may not be the primary factor responsible for selection, but rather some other factor indirectly related to size. Keast and Webb (1966) suggested that mouth size be studied because morphological limitations of the feeding apparatus determine the size and type of prey that can be handled.

Differences in contrast between food items may alter the detection of prey by fish. Within the cladocerans, stickleback selected bosminids and sidids, but not chydorids. Bosminidae and Sididae are relatively transparent except for their dark compound eyes which may influence the distance at which they are sighted by predators. Similarly, Zaret and Kerfoot (1975) reported that Melaniris (silversides) select individual Bosmina longirostris, (Muller) on the basis of eye pigmentation rather than total body length.

In addition to contrast, selection for the relatively large sidids and chironomid larvae and conspicuous bosminids may be explained by their greater reactive distance relative to other available prey. From the perspective of the predator, reactive distance (the maximum distance at which the predator can locate a specific prey) is a crucial element in searching for prey (O'Brien 1979). Reactive distance has been measured independently several times (Werner and Hall 1974, Confer and Blades 1975 and Vinyard and O'Brien 1976) and has always been found to increase linearly with increasing prey length, and to be dependent on illumination (Vinyard and O'Brien 1976).

Copepods may be avoided by stickleback because of the energy expenditure required to capture them. Less evasive chironomids, ostracods and cladocerans were selected when abundant and cyclopoids only consumed in significant amounts when abundance of food was low (in April, consistent with optimal foraging theory) and reduced temperatures in winter lower the evasive ability of cyclopoids (O'Brien 1979). Drenner _et al._ (1978) investigated the role of zooplankter escape in selective feeding. Zooplankters are capable of using mechanoreceptors to percieve hydrodynamic disturbances and are thus able to avoid suction and shear fields (Strickler 1975 _in_ Drenner _et al._ 1978). Capture probabilities are greatest for cladocerans, intermediate for cyclopoid copepods and lowest for diaptomid copepods and _Chaoborus_ (Drenner _et al._ 1978, O'Brien 1979, and Confer and Blades 1975). Capture probability is probably the dominant event determining selectivity of non-visual feeders. Although differential encounter and attack probability are dominant factors determining selectivity of visual feeders, capture probabilities are influential. Vinyard (1980) has shown that bluegill sunfish (_Lepomis_ macrochirus) are capable of modifying both their prey selectivity and capture behavior to increase return. Sunfish restricted predation to the nonevasive Daphnia (optimal foraging) until the size of the evasive Diaptomus was two times greater (prey size maximizer).

Prey motion may further augment the selectivity of Culaea for cladocerans rather than copepods. Cladocerans move constantly whereas copepods move intermittently. Because of the poor image transmitting properties of water visual acuity may only be achieved in a relatively close field, therefore motion, which increases the reactive distance (Ware 1973), is often crucial for detection and recognition of prey. Not only motion, but quality of motion is significant (Hyatt 1979). Brooks (1968) and Vinyard (1980) reported that fish chose Daphnia over diaptomid copepods of a similar size because their patterns of motion are different.

Sticklebacks have taste receptors on their lips and in their pharynx, buccal cavity and esophagus which also may play a role in the selection of food (Wootton 1976). Beukema (1968) and Wootton (1976) suggested that palatability may have an effect on the feeding behavior of Gasterosteus aculeatus. When a food item was taken by a three-spined stickleback the fish tended to increase the intensity of search in that area but when a prey was rejected the fish left the area (Thomas 1974).

Selection may be dependent on the food value (Rozin and Mayer 1961) and nutrient requirements (Gibb 1962 and Tinbergen 1960 in Schoener 1971) of the fish. The food items of the stickleback in decreasing caloric value (obtained from Cummins and Wuycheck 1971) per g ash free dry wt are: Cyclopoida (5778), Chydoridae (5609), Bosminidae (5534), simuliid larvae (5521), chironomid larvae (5355) and Daphnia (5292). Although cyclopoids and chydorids have a greater caloric value, the increase in the food value obtained is probably outweighed by the greater energetic costs to capture them. Less valuable as well as less costly items, Bosminidae, Simuliidae and Chironomidae, may be selected instead.

Foraging behavior. Due to poor visibility in the Bog and Rennie Rivers, observations on feeding behavior of brook stickleback were made at a site of similar geographical and physical characteristics in the Brokenhead River. Observations were made on stickleback occurring in the stream center as access to fish in stream margins was restricted by dense vegetation.

According to optimal foraging theory natural selection has produced animals whose foraging behavior maximizes their fitness and therefore they should possess a repertoire of foraging procedures that also maximize energy yield (Hyatt 1979). The composition of the stickleback diet is the result of interactions of predator morphology, behavior, preference and food handling.

When stickleback feed, the premaxillae are protruded and food is sucked in by expansion of the buccal and opercular cavities as the mouth closes (Alexander 1967). Considering the foraging behavior and diet of stickleback there are several advantages to protruding the premaxillae (Wootton 1976); the mouth is brought closer to the food item so it has less chance of escape, the fish does not have to take such an oblique stance to capture prey on the bottom, the angle of the mouth is reduced so the jaws can be closed more quickly, and protrusion allows the food to be held straight making swallowing easier.

Feeding phases have been previously observed for Culaea by MacPhail and Lindsey (1970) and for Gasterosteus aculeatus (Tugendhat 1960). The interpretation of stickleback foraging behavior as a series of sequential phases consisting of swim, hover, aim, dart and handle is useful because each phase can be analysed separately. Although inherent among stickleback the sequence of phases was not fixed. Any or all of the phases preceeding the dart may be omitted. Flexibility of the sequence is adaptive for feeding on prey whose abundance and distribution are unpredictable. The exclusion of the active searching response in 32.8% of the feeding sequences suggests stickleback were minimizing time and energy expenditure by feeding on dense clumps of prey when available. Omitting hover, the most time consuming phase, in 60% of the sequences beginning with swim supports the interpretation of

Culaea as a time minimizer. Sticklebacks are capable of modifying feeding behavior depending on the distribution of prey in order to maximize energy yield.

Some form of decision prior to capture occurs as indicated by the high rate of terminated phases (e.g. 47.9% and 40.4% for hover and aim respectively).

Initial choice occurs in the hovering phase; predators may choose whether or not to pursue a prey or which prey to pursue. Fish are capable of recognizing prey and determining difficulty of capture from previous experience (Vinyard 1980). If the stickleback decides to give pursuit it may still reevaluate the prey and decide not to attack during the aim phase. Stickleback minimize time and energy expenditure by not pursuing prey they cannot catch and not attacking prey they cannot handle. The efficiency of the foraging strategy is such that when the stickleback finally attacks a prey, the probability of capture is very high (96%). Although quantitative analysis of handling was not possible, field observations indicate stickleback were successful in ingesting almost all prey captured.

CONCLUSION

Brook stickleback maximized foraging efficiency by living and feeding in vegetated areas where prey were abundant and vegetation provided protection from predators while feeding. Stickleback fed primarily during daylight hours when visual detection of prey was optimal. Diet was potentially optimized by selecting particular taxa and sizes within taxa for which the probability of capture and handling was high. Stickleback minimized foraging time by modifying feeding behavior to eliminate particular phases depending on the distribution of prey thereby increasing time for other activities (e.g. defending teritories, predator avoidance, and monitoring mates).

Optimal foraging theory is useful in interpreting foraging strategies of brook stickleback. Conformity with the predictions of optimal foraging theory supports the argument that time and energy are the main factors for the feeding patterns observed. Brook stickleback forage so as to maximize the net rate of energy intake. Occasional disagreements with the predictions of optimal foraging might be explained by constraints of the natural environment (e.g. competition, predator avoidance, and nutrient demands) not incorporated in optimal foraging models.

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Appendix 1

Age class determination

Two age groups, young of the year (0) and adults (1+) were distinguished by length frequency distributions using probability paper. Standard length ($\pm$ 0.01 mm) was recorded for each fish and length frequencies arranged in size classes of 5 mm. Monthly cumulative percent frequencies were calculated for each site from June to October, 1979 and plotted on probability paper (Cassie, 1954). Points of inflexion on the resulting curve indicate troughs between normal distributions. Since the troughs represent an overlapping of two size classes, the distributions were cut off at the points of inflexion to define the ranges of the size classes. Comparisons were made between the resultant size classes and size frequency distributions to ensure false size classes were not created.

Length frequency distributions (Table A) reveal three age groups of Culaea inconstans inhabiting The Bog and Rennie Rivers during this study. In June, 1979 the population consisted of predominantly age 1 fish and a few age 2+ fish. Age 0 fish were first observed in July and thereafter formed the bulk of the population. As there were few age 2+ fish present, they were combined with the age 1 fish and are collectively referred to as adults or age 1+.

The mean standard length of young of the year fish, varied from 20.2 mm in July to 32.3 mm in October. The mean standard length of adult fish varied from 33.6 mm in June to 42.5 mm in October. As the mean standard length of age 0 fish in October is comparable to that of age 1+ fish in June, fish of this length will be considered adult (Table B).

Table A. Length frequency distributions of brook stickleback at 3 sites from June to October 1979.

Month	Size Class Mean (mm) 12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	n
June	2	85	188	69	26	9	2	-	-	381
July	34	121	117	32	102	105	62	6	-	579
August	2	59	106	98	65	93	47	24	4	498
September	-	-	12	55	37	26	18	8	1	157
October	-	-	5	14	12	16	11	2	-	60

Table B. Mean standard length (mm) of age 0 and 1+ stickleback from June to October, 1979.

	Month				
	June	July	August	September	October
mean age 0	-	20.2	24.4	30.3	32.3
range age 0	-	11.2-28.0	12.7-32.9	20.4-38.0	20.9-39.9
mean age 1+	33	34.6	36.8	41.9	42.5
range age 1+	24.3-51.0	28.2-47.5	33.1-47.2	38.0-51.2	38.5-48.1

Appendix 2

The variance to mean ratio, $\frac{s^2}{\bar{X}}$ (n - 1), of the predominant invertebrates in 4 subsamples were compared with the χ^2 distribution for 3 samples. With 3 degrees of freedom at the 5% level of significance $\chi^2 = 7.815$. For each food category, the difference between the variance and mean was non-significant, therefore the subsampling technique was adequate.

Food Category	$\frac{s^2}{\bar{X}}$ (n - 1)		
	1	2	3
Ostracoda	1.7**	1.6**	3.3*
Chironomidae	2.2**	2.0**	2.5*
Cyclopoida	1.0**	2.6*	1.7**
Chydoridae	3.1*	3.6*	5.1*

Note: *, $p < 0.10$; **, $p < 0.50$

Appendix 3. Feeding indices of age 0 and 1+ stickleback by site. Number of fish examined ranged from 4-60 (* n < 4).

Site	Month	Age	Time of Day (h)						
			0400	0800[1]	1200	1600	2000	2400	Average
1.	April	1+			0.3				0.3
	May	1+		1.1	1.5	1.8	2.6		1.7
	June	1+	0.1	0.8	2.2	2.6	1.7	1.1	1.4
	July	0	1.0	1.5	1.7	1.6	2.6	2.1	1.7
		1+	0.2	0.8	1.0	1.2	1.5	1.3	1.0
	August	0	0.4	0.9	2.1	2.0	2.3	1.5	1.8
		1+	0.2	0.6	1.6	1.6	1.7	0.8	1.1
	September	0		0.1	1.3	1.0			0.8
		1+		0.3*	1.6	1.3			1.1
	October	0			1.0				1.0
		1+			0.8				0.8
2.	April	1+			0.4				0.4
	May	1+		1.8	1.5	1.0	3.0		1.8
	June	1+	0.3	1.0	1.4	1.1	1.2	0.7	1.0
	July	0	0.3	1.2*	1.3*	2.3*	1.1	1.3*	1.2
		1+	0.1	0.7	0.7	1.0	0.4	0.2	0.5
	August	0	0.1*	0.9*	1.4*	1.9*	1.4*	0.5*	1.1
		1+	0.1	0.7	0.8	1.0	0.7	0.2	0.6
	September	0		0.4	0.8	1.4			0.9
		1+		0.2	0.5	1.1			0.6
	October	0			1.4				1.4
		1+			0.5				0.5
3.	April	1+			2.2				2.2
	May	1+		1.2	0.9	0.9	1.9		1.2
	June	1+	0.4	1.1	1.6	1.6	1.3	0.6	1.1
	July	0	0.2	2.0	1.9	1.8	2.2	1.2*	1.6
		1+	0	0.6	0.7	0.8*	1.1	0.6	0.6
	August	0	0*	1.2	1.3	1.0*	1.8	1.0*	1.1
		1+	0*	0.4	0.9	0.9	0.8	0.4	0.6
	September	0		0.5	1.1	0.9			0.8
		1+		0.1	0.8	1.7			0.9
	October	0			0.8				
		1+			0.6				

[1] In September fish were collected at 0600 hrs.

Appendix 4. Mean number of food items per stomach of age 0 and 1+ stickleback, by month for each site. n ranges from 10 to 25 (* n<10).

	Month											
	April	May	June	July		August		September		October		Winter
	1+	1+	1+	0	1+	0	1+	0	1+	0*	1+*	1+
1												
Cyclopoida	6.4	27.4	13.1	9.2	11.5	6.9	9.3	8.7	8.2	23.5	36.4	0.5
Harpacticoida	1.6	1.4	6.7	0.4	0.5	0.1	0.1		0.1	1.5	12.5	
Chydoridae		6.2	18.5	1.5	3.1	2.1	1.8	9.1	9.5	46.0	30.3	
Sididae	0.1	0.8	0.2	1.8	1.8	20.7	8.2	1.8	2.1		0.5	
Bosminidae					0.1	4.0	18.0	2.5	2.7	0.5	0.1	
Daphnidae		0.4	0.1	0.3	0.3	0.5	0.9	1.3	2.1		0.8	
Ostracoda	0.2	9.7	27.1	5.5	6.6	1.1	2.7	1.4	4.2	0.5	0.9	
Chironomidae l.	2.0	13.4	17.9	12.0	18.1	8.3	18.4	8.5	16.1	5.0	24.4	0.9
Simuliidae l.		2.0	0.5									
Other	1.1	5.3	6.5	5.0	6.0	1.3	4.2	0.9	2.5	1.5	4.1	0.1
2												
Cyclopoida	9.8	4.7	5.6	2.8	5.3	1.9	1.3	4.7	3.6	3.3	14.4	1.3
Harpacticoida	0.7	1.0	31.9	0.1	0.4			0.1	0.1	0.3	0.9	
Chydoridae		1.6	12.6	46.6	100.2	40.8	24.6	27.1	23.2	3.0	17.1	
Sididae			0.2	0.6	0.4	0.4	0.6	1.1	1.4		0.4	
Bosminidae				8.3	0.4			0.1	0.1		0.4	
Daphnidae		0.2	0.1	0.3		0.2	0.1	0.5	0.6		0.6	
Ostracoda		0.3	8.7	7.3	5.9	3.9	2.4	0.3	1.1		0.9	
Chironomidae l.	5.2	26.5	7.7	18.0	29.1	10.6	16.4	9.9	7.0	4.7	15.1	0.9
Simuliidae l.		38.2	2.0									
Other	0.5	4.1	6.1	16.4	3.1	0.8	3.0	3.2	3.4	2.7	7.1	
3												
Cyclopoida	3.1	4.5	19.7	6.8	6.2	4.9	3.1	4.6	3.7	6.0	5.0	
Harpacticoida	0.9	1.5	9.7			0.1						
Chydoridae		6.0	37.8	5.8	7.0	6.2	6.1	15.8	12.8	26.0	5.8	
Sididae		0.1	0.4	2.2	0.7	4.3	2.3	1.1	1.3			
Bosminidae			11.4	12.9	13.5	7.2	2.2	0.2		2.0	0.4	
Daphnidae		0.2	0.2	2.9	0.6	0.3	0.3	0.3	0.5	0.5		
Ostracoda			23.8	1.3	1.2	4.0	1.6	2.1	1.7	0.4	0.4	
Chironomidae l.	10.2	13.1	9.5	24.6	67.8	8.8	18.5	8.7	15.2	43.6	14.0	
Simuliidae l.		0.7										
Other	3.9	2.9	4.1	1.9	5.0	1.9	4.8	5.3	4.0	7.8	2.6	

Note: l., larvae

Appendix 5. Percent composition of stomach contents by month for 0 and 1+ age class stickleback for each site. Values based on at least 10 fish (n < 10 for October).

Food Category	April	May	June	July		August		September		October	
	1+	1+	1+	0	1+	0	1+	0	1+	1	1+
1											
Cyclopoida	56.1	42.1	15.5	25.8	23.6	15.4	14.6	25.4	17.5	29.9	33.1
Harpacticoida	14.0	2.3	6.6	1.2	1.0	0.1	0.2	0	0.2	1.9	11.4
Chydoridae	0	9.7	17.3	4.2	6.4	4.7	2.9	26.5	20.5	58.6	27.5
Sididae	0.9	1.0	0.6	5.0	3.6	46.2	12.8	5.2	4.5	0	0.5
Bosminidae	0	0.1	0	0	0.2	8.9	28.3	7.4	5.8	0.6	0.1
Daphnidae	0	0.6	0.1	0.8	0.7	1.1	1.4	3.8	4.5	0	0.7
Ostracoda	1.7	11.4	24.5	15.4	13.5	2.3	4.3	4.0	9.0	0.6	0.8
Chironomidae l.	17.5	20.0	19.3	33.6	37.2	18.4	29.0	24.9	34.5	6.4	22.2
Simuliidae l.	0	4.4	0.7	0	0	0	0	0	0	0	0
Other	9.8	8.4	15.4	14	13.8	2.9	6.5	2.8	3.5	2.0	3.7
2											
Cyclopoida	59.4	5.6	5.8	2.6	3.7	3.2	2.8	10.0	8.9	23.8	25.3
Harpacticoida	4.0	1.2	24.2	0.1	0.3	0	0.1	0.1	0.2	2.4	1.5
Chydoridae	0	2.5	25.0	43.6	69.2	69.6	50.6	57.7	57.5	21.4	30.1
Sididae	0	0	0.1	0.5	0.3	0.8	1.2	2.3	3.5	0	0.8
Bosminidae	0	0	0.1	7.7	0.3	0	0	0.1	0.2	0	0.8
Daphnidae	0	0.3	0	0.2	0	0.4	0.2	1.0	1.4	0	1.0
Ostracoda	0	0.5	11.9	6.8	4.1	6.6	4.9	0.7	2.7	0	1.5
Chironomidae l.	31.7	40.7	16.0	16.9	20.1	18.0	33.8	21.1	17.2	33.3	26.6
Simuliidae l.	0	43.6	6.0	0	0	0	0	0	0	0	0
Other	4.9	5.6	10.9	21.6	4.0	1.4	6.4	7.0	8.4	19.1	12.4
3											
Cyclopoida	17.0	14.5	17.5	11.7	6.1	13.0	7.9	12.0	9.4	6.6	17.7
Harpacticoida	4.9	5.0	2.2	0	0	0.3	0	0	0	0	0
Chydoridae	0	18.9	28.9	9.9	6.9	16.5	15.8	41.7	32.7	34.2	20.6
Sididae	0	0.1	0.2	3.7	0.7	11.3	5.8	2.8	3.2	0	0
Bosminidae	0	0.2	22.9	22.1	13.3	19.2	5.7	0.4	0	2.2	1.4
Daphnidae	0	0.8	0.1	5.0	0.5	0.7	0.9	0.7	1.3	0.2	0
Ostracoda	0	7.0	15.5	2.2	1.1	10.7	4.2	5.4	4.3	0.4	1.4
Chironomidae l.	56.0	40.9	11.9	42.2	60.6	23.3	47.6	22.9	38.9	47.8	49.6
Simuliidae l.	0	2.2	0	0	0	0	0	0	0	0	0
Other	22.1	10.4	0.8	4.7	10.8	5.0	12.1	13.7	10.2	8.6	9.3

Note: l, larvae

Appendix 6. Density (number·L^{-1}) of food organisms in the environment by month for each site.

Food Category	Month						
	April	May	June	July	August	September	October
1.							
Cyclopoida	0.8	55.9	12.4	34.4	69.1	32.6	26.7
Harpacticoida		2.1	0.7	0.2	0.9	0.2	1.5
Chydoridae	0.5	11.6	13.9	8.7	18.5	20.3	14.4
Sididae		0.8	0.3	3.1	30.0	0.9	
Bosminidae				0.8	1.8	0.4	
Daphnidae			0.1		4.5	0.3	0.3
Ostracoda	0.3	16.0	8.4	34.4	12.4	1.1	4.1
Chironomidae l.	0.6	8.7	3.3	21.1	29.8	18.7	3.1
Simuliidae l.		0.9		0.5			
Other	3.3	18.6	2.5	27.6	19.1	7.5	3.2
2.							
Cyclopoida		5.1	1.1	15.3	11.6	24.1	9.3
Harpacticoida		0.9	0.3				1.2
Chydoridae	0.1	2.3	8.3	37.9	80.9	102.4	10.1
Sididae			0.1	1.1	1.0	4.5	
Bosminidae			0.3	3.7	0.2	0.3	
Daphnidae				1.8	0.7	1.5	
Ostracoda		2.9	1.6	6.9	6.4	8.7	0.8
Chironomidae l.	1.0	4.8	4.4	17.3	29.3	83.9	8.5
Simuliidae l.	0.5	6.8	0.1				
Other	0.3	5.7	2.7	15.9	8.6	8.5	4.2
3.							
Cyclopoids	2.9	9.9	53.1	48.0	68.0	67.3	5.9
Harpacticoida	3.1	0.5	0.9	0.1			
Chydoridae		3.3	43.6	37.1	38.5	28.7	13.7
Sididae			0.2	4.2	10.7	0.6	
Bosminidae		0.1	1.7	19.6	1.0	0.4	
Daphnidae			0.7	12.9	4.4	0.1	
Ostracoda	0.8	1.1	15.1	5.0	6.3	0.9	
Chironomidae l.		2.7	23.7	24.3	33.6	21.6	9.7
Simuliidae l.		0.3	0.4				
Other	19.3	14.9	10.2	31.3	15.2	9.0	4.4

Note: l., larvae

Appendix 7. Percent composition of food items in the environment by month for each site. Percentages based on 4 replicates (*, n = 1; **, n = 3).

Food Category	April*	May	June	July	August	September**	October *
1.							
Cyclopoida	14.9	48.1	28.5	31.0	37.8	0.6	50.1
Harpacticoida	0	1.5	1.7	0.1	0.4	1.4	2.9
Chydoridae	9.8	9.9	34.2	10.8	9.2	0.2	26.9
Sididae	0	0.7	0.5	2.7	16.0	5.8	0
Bosminidae	0	0	0	0.6	1.2	0	0
Daphnidae	0	0	0.3	0	2.6	6.2	0.5
Ostracoda	5.0	13.8	18.9	13.5	6.6	2.8	7.7
Chironomidae l.	10.0	7.1	7.3	17.8	16.7	50.3	5.8
Simuliidae l.	0	0.9	0	0.4	0	0	0
Other	60.3	18.0	8.6	23.1	9.8	32.7	6.1
2.							
Cyclopoida	0	32.8	5.8	15.0	9.5	10.7	27.3
Harpacticoida	0	1.8	3.3	0	0	0	3.6
Chydoridae	4.4	9.4	44.7	37.6	57.0	43.0	29.7
Sididae	0	0	0.8	1.2	0.7	1.9	0
Bosminidae	0	0.2	0.5	3.5	0.2	0.1	0
Daphnidae	0	0	0.1	1.8	0.4	0.6	0
Ostracoda	0	3.7	6.7	7.4	4.2	3.7	2.4
Chironomidae l.	51.9	9.4	22.8	18.0	21.4	36.1	24.9
Simuliidae l.	26.0	0.9	0.7	0	0	0	0
Other	17.7	41.8	14.6	15.5	6.6	3.9	12.1
3.							
Cyclopoida	11.1	32.8	35.8	25.6	37.3	53.3	17.5
Harpacticoida	11.8	1.8	1.3	0	0	0	0
Chydoridae	0	9.4	29.7	19.5	21.4	21.5	40.7
Sididae	0	0	0.6	2.5	5.9	0.4	0
Bosminidae	0	0.2	1.2	11.7	0.6	0.2	0
Daphnidae	0	0	0.4	5.9	2.5	0.1	0
Ostracoda	3.0	3.7	8.2	2.6	3.4	0.7	0
Chironomidae l.	0	9.4	12.3	14.3	19.2	16.6	28.8
Simuliidae l.	0	0.9	0	0	0	0	0
Other	74.1	41.8	10.5	17.9	9.7	7.2	13.0

Note: l., larvae