Size-Structured Mortality in a Threespine Stickleback (*Gasterosteus aculeatus*) – Cutthroat Trout (*Oncorhynchus clarki*) Community

T. E. Reimchen

Department of Zoology, University of Alberta, Edmonton, Alta T6G 2E9 Canada

Reimchen, T. E. 1990. Size-structured mortality in a threespine stickleback (*Gasterosteus aculeatus*) – cutthroat trout (*Oncorhynchus clarki*) community. Can. J. Fish. Aquat. Sci. 47: 1194–1205.

In a 112-ha bog lake on the Queen Charlotte Islands, British Columbia, small fish comprised the major element in the diet of cutthroat trout (*Oncorhynchus clarki*). Despite the presence of juvenile salmon and char in the lake, threespine stickleback (*Gasterosteus aculeatus*) was the most common fish in the diet (99.5%). Foraging activity appeared to be more frequent in littoral than in limnetic regions. Mark–recapture methods indicate an average population of 220 trout and 75 000 adult stickleback. Trout consumed an estimated 308 770 stickleback yearly (145 kg) of which 65% were taken during summer. Seventy-three percent of all fish consumed were young of the year and 2% were adults, the latter representing 4% of the adult population in the lake. There was a 75% reduction in total mortality between successive year classes of stickleback (0,1,2,3+). This consumption curve, which resembles a typical survivorship curve of fish, is a function of the size-structure of the populations and includes interactions between size availability of stickleback, prey-size preferences of the trout, and length frequency distributions of trout. Total weight of stickleback consumed by trout comprised about 40% of that previously calculated for 16 species of avian piscivores in the lake.

Dans un lac-tourbière de 112 ha des îles Reine-Charlotte (Colombie-Britannique), les petits poissons constituent l'élément principal du régime alimentaire de la truite fardée (*Oncorhynchus clarki*). Malgré la présence de salmonidés juvéniles dans le lac, l'épinoche (*Gasterosteus aculeatus*) est la principale proie (99,5%). La recherche de nourriture semblait plus fréquente dans la région littorale que dans la région limnétique. Les résultats d'expériences de marquage et de recapture révèlent une population moyenne de 220 truites et de 75 000 épinoches adultes. La truite consommait environ 308 770 épinoches par an (145 kg) dont 65% étaient capturées à l'été. Soixante-treize pour cent de tous les poissons consommés étaient des nourrains et 2% étaient des adultes qui constituaient 4% de la population adulte peuplant le lac. On a noté une baisse de 75% du taux de mortalité total entre des classes annuelles successives d'épinoches (0, 1, 2, 3+). La courbe de consommation, qui ressemble à une courbe typique de survie du poisson, est une fonction de la structure des tailles chez les populations et comprend des interactions entre la disponibilité de chaque taille d'épinoches, les préférences de la truite quant à la taille de la proie et les distributions de la fréquence des longueurs de la truite. Le poids total des épinoches consommées par la truite représente environ 40% du poids total calculé pour 16 espèces d'oiseaux piscivores fréquentant le lac.

Received May 23, 1989
Accepted January 18, 1990
(JA173)

Reçu le 23 mai 1989
Accepté le 18 janvier 1990

Integration of natural history, theory, and experimentation have advanced our understanding of the dynamics of predator–prey interactions (for example, Werner et al. 1983; Taylor 1984). Although not discussed in recent evolutionary syntheses (Futuyma 1979; Endler 1986; Feder and Lauder 1986), one substantive deficiency in an otherwise extensive literature on predator–prey interactions are data on sources and extent of mortality throughout the survivorship curve of the prey. Such information is fundamental in assessing interpopulation and ontogenetic differences in prey defenses.

The threespine stickleback (*Gasterosteus aculeatus*) has been used in numerous behavioral and morphological studies over the last 50 yr (for reviews see Wootton 1984; Bell 1984). Differences in phenotypic traits frequently occur between populations and are occasionally associated with presence or absence of predators (Hagen and Gilbertson 1972; Moodie 1972; Moodie and Reimchen 1976; McPhail 1977; Gross 1978; Reimchen 1980; Giles and Huntingford 1984). This species is a logical candidate for studies of sources and extent of age-specific mortality. As part of a long-term investigation of intra-population variability in prey defenses in the threespine stickleback, I undertook such an evaluation in an ecologically undisturbed population. These ongoing studies (Reimchen 1983, 1988, 1990) show a complex of at least 21 species of avian, salmonid, mammalian, and invertebrate piscivores. Fourteen species of avian piscivores consume from 295–573 kg fish·y^{-1}, most of which are probably stickleback (Reimchen and Douglas 1984). In this paper, I focus on the most common predatory fish in the lake, cutthroat trout (*Oncorhynchus clarki*), and quantify diet and age-specific predation of stickleback. To provide a realistic estimate of consumption, data were collected on seasonal differences in (a) foraging rates of the predator, (b) population size and length distribution of predator, (c) dietary proportion of prey items for each length class of predator, and (d) length frequency distributions of the prey eaten by each size-class of the predator.

Methods

Study area

The study was carried out at Drizzle Lake (112 ha, elevation 55 m), Queen Charlotte Islands, British Columbia. Historically,

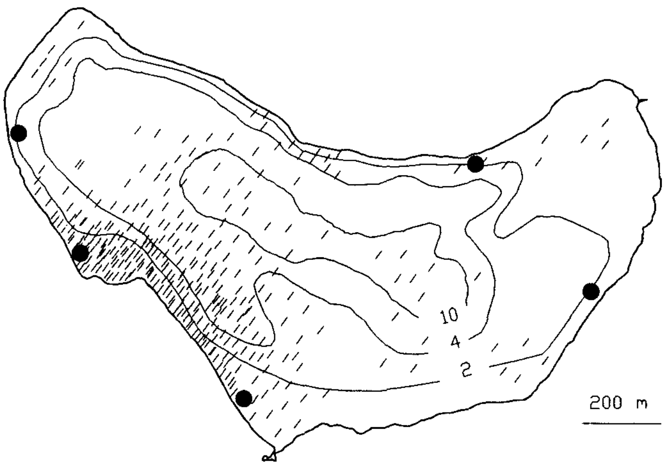

FIG. 1. Bathymetric map of Drizzle Lake showing locations of fyke net (●) and gill net (/). Depth contours in meters.

this remote watershed has received negligible disturbance from human activity and is currently protected under the Ecological Reserves Act (Krajina et al. 1978). General habitat of this watershed has been described (Reimchen and Douglas 1980, 1984; Stinson 1982). The substratum in Drizzle Lake is a combination of coarse sand, gravel, and small boulders (generally less than 15 cm in diameter). Since it is a dystrophic and deeply coloured lake (transmission at 400 nm =67%, Reimchen 1989), aquatic macrophytes are uncommon, apart from several shallow bays where the water lily (*Nuphar luteum*) achieves moderate densities (1 plant/3 m^2). Small submerged plants (*Eleocharis, Juncus,* and *Lilaeopsis*) occur near shoreline in low abundance. Foraging cover, such as fallen trees and other submerged debris, is uncommon. Bathymetry is relatively simple with gentle gradients on most of the perimeter except the central northern area where it drops off more steeply (Fig. 1).

There are resident populations of threespine stickleback, cutthroat trout, Dolly Varden (*Salvelinus malma*), and coho fry (*Oncorhynchus kisutch*) in the lake. Sixteen species of avian piscivores have been observed over a 5-yr period (Reimchen and Douglas 1984). River Otter (*Lutra canadensis*) occasionally enter the lake from adjacent streams. The stickleback are characterized by extensive melanism, exceptionally large adult body size (70–110 mm) with stout dorsal and pelvic spines (Reimchen et al. 1985) and are similar to the endemic black stickleback initially described for Mayer Lake (Moodie 1972) which occurs 20 km to the south.

Estimating Population Size and Size Distribution

Ascertaining the actual number of trout in the lake at any single time poses several difficulties. Small trout (<15 cm) enter the lake from inlet streams usually with coho salmon fry in spring. Some move directly into the outlet stream while others remain in the lake. The latter are subject to predation from diving birds. Larger trout also move into the outlet stream for periods up to 6 mo before returning to the lake (judged by the recapture incidence of marked fish). Given these constraints, numbers of cutthroat trout (hereafter, trout) in the lake were estimated with mark–recapture studies from 1983–85 and in 1988. A standard fyke net (hoop diameter 1.5 m, mesh 5 mm) was set primarily in littoral regions of the lake since the previous period of gillnetting (1976–83) indicated most activity close to shore. Those set in limnetic regions rarely yielded fish which is largely a consequence of the poor capture efficiency of this net in open water. Hoops were generally set at 1.5–2 m water depth. A seine net (with additional floats attached to the float line) was attached to the hoop and extended to the shoreline from the edge of the trap entrance. The fyke net was left undisturbed generally for 3–4 d (range 1–7) and then raised and the fish removed and counted. Trout were measured for standard length, marked and released. The net was then reset at a different site on the lake (Fig. 1). Throughout the study, marked fish were often recaptured within 3 d of their release on the opposite side of the lake indicating extensive movement and shoreline dispersal. I gill-netted in the central parts of the lake on several occasions during the marking program to determine whether there was dispersal of marked fish from littoral into limnetic regions; of three fish netted, two were recaptures, indicating mixing of inshore and offshore trout. Total collecting time with the Fyke net was 148 d in 1983, 246 d in 1984, 173 d in 1985, and 80 d in 1988.

For most marking techniques, I used a nylon line with colored beads placed through the dorsal musculature at the insertion of the dorsal fin. During 1983–85, the color of the beads was changed every 2–3 mo on unmarked fish while in 1988, trout were marked with individually identifiable tags. During the first year of marking, about one-third of the tags were lost. In these cases, I was still able to identify a general recapture by the two small holes or healed skin at the insertion site although I was not able to place the fish within any specific marked group. The marking procedure was modified by producing a loop to the nylon line which was knotted and fused. Tag loss was largely eliminated (<5%). Several methods were used for estimating population size. For most purposes, I employ a sequential series of independent Petersen's estimates (based on monthly mark–recapture data) to arrive at a best fit curve of population numbers over the year (equations 3.7 and 3.8, Ricker 1958). These estimates are compared with those derived using Schnabel and Jolly-Seber methods (Seber 1982).

Detailed methodology for estimating population size of stickleback in the lake will be presented separately but a brief description follows here. In spring 1985, 17 033 adult stickleback (SL 70–95 mm) were marked and released throughout the lake, of which 3803 were recaptured in summer. Based on both Petersen's and Schnabel's methods, population estimates of adult stickleback ranged from 30 000 to 120 000 ($\bar{x}=75\ 000$). Nest densities and numbers of breeding males in different littoral areas were recorded; I estimated there to be 10 000–60 000 nests over the 3-mo breeding season with an average of 395 eggs per nest (range 166–1014, $N=32$). Assuming the occurrence of 30 000 nests and complete hatch, recruitment would be 12 million fry. Because of egg consumption by some adult stickleback (16.4%) and cannibalism of fry by a low percentage of adults (3%), sub-adults (1.5%) and juveniles (0.2%), as well as whole-nest predation by Dolly Varden (Reimchen 1990), a substantial but unknown proportion of the 12 million potential recruitment will be lost.

Evaluating Diet

Trout (>10 cm) were captured with a variety of monofilament gill nets (10–100 mm stretch mesh diameter, usually 20 m total length) set in a diversity of localities throughout the lake from 1976 to 1983 (Fig. 1). I did not net during periods of extensive lake occupancy by diving birds in mid-summer or

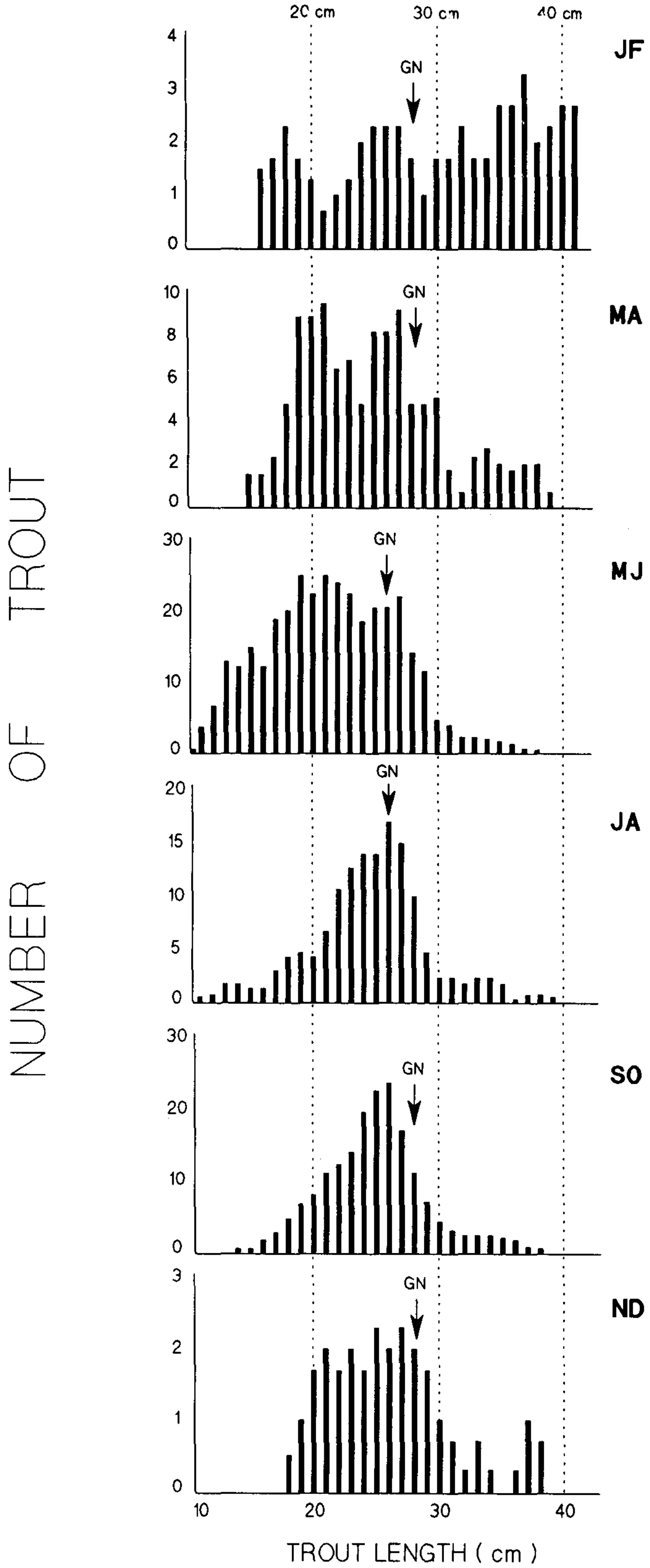

FIG. 2. Standard length of trout captured in fyke net at bimonthly intervals (1983–85). Histogram shows three-point moving average for 1-cm length-groups in raw data. GN = mean size of trout captured in gill nets (1976–83).

during ice cover which occurred irregularly from November to March. Because numbers of trout in the lake were unknown, I generally limited the gill-netting period to obtain, on average, a single trout per week throughout the year suspecting that this was a very conservative exploitation rate for a 112-ha lake. As population estimates of trout were later to demonstrate, even this exploitation rate was high.

Gill nets were generally checked near dawn and again several hours prior to dusk. Standard length of trout was recorded to the nearest centimetre and the stomach contents preserved in formaldehyde. Prey in the stomachs were identified (invertebrates to order, fish to species where possible) and numbers of each fish prey determined. I made visual estimates of the relative volume of the major taxa in the stomachs. Beginning in autumn 1979, intact fish prey were measured for standard length. Undigested stickleback spines, occasionally with tissues attached, were common in the pyloric region of the stomach; I measured length of these spines under a dissecting scope equipped with an ocular micrometer. Left and right pelvic spines were differentiated to allow determination of numbers of stickleback eaten per fish. Spine length and body length were determined on a sample of living stickleback to establish the regression equation from which original body sizes of stickleback in the trout stomachs were reconstructed.

Estimating Total food Consumption

Water temperature and body weight are the two major variables in calculating optimal daily food rations for trout (Elliott and Persson 1978). Accordingly, lake temperature was recorded (100 m from shore, 0.1 m below surface, 1200 h) monthly for 2 yr (1984, 1985). I tabulated the length distribution of trout collected in the fyke net during bimonthly periods (1983–85). Based on the monthly population estimates of trout, I calculated for each 1-cm length class the predicted numbers of trout in the lake of this size-class. To obtain a conversion from length to weight (required for estimating daily food requirements), I weighed 124 trout to the nearest 10 g over a range of standard lengths (120–400 mm) during the 1988 marking program. This yielded the least squares regression:

[1] $W = 0.000007821 \cdot L^{3.0626}$,

where W = weight of trout (g) and L = standard length of trout (mm) (intercept = −11.76, $r^2 = 0.95$, $p < 0.001$). Weights were estimated for each 1-cm length-class of trout.

A length-weight relationship was determined for stickleback (size range 12–90 mm). Moist individuals ($N = 102$) were measured for standard length and weighed (± 0.001 g) on an electronic balance. This produced the regression:

[2] $W = 0.000006803 \cdot L^{3.121}$,

where W = weight (g) and L = length (mm) (intercept = −11.9, $r^2 = 0.99$, $p < 0.001$). I used the following length and weight groups: 7–9 mm = 0.005 g, 10–14 mm = 0.016 g, 15–19 mm = 0.047 g, 20–29 mm = 0.157 g, 30–39 mm = 0.45 g, 40–49 mm = 0.98 g, 50–59 mm = 1.84 g, 60–69 mm = 3.09 g, 70–79 mm = 4.83 g, > = 80 mm = 7.14 g.

These and additional equations (see below) were combined with all variables (Table 3) into a general computer program to determine monthly stickleback consumption (weight, numbers, and size-specific numbers).

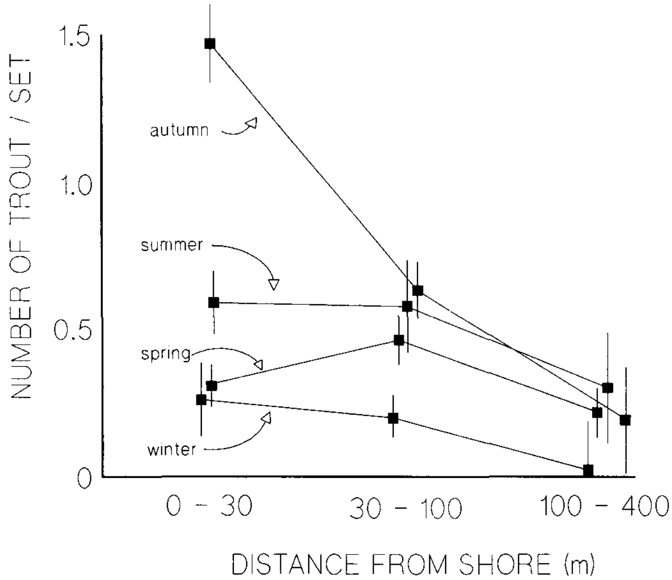

FIG. 3. Gill net effort (mean number of trout per set) at Drizzle Lake (1979–83) in relation to lake position and season. Number of sets in each lake position are 229, 290, and 137, respectively. Number of sets for winter, spring, summer, and autumn are 168, 254, 111, and 123, respectively.

Results

Population Characteristics of Trout and Stickleback

Standard length of trout captured in the fyke net ranged from 10–41 cm with a mode at 22 cm. Bimonthly frequencies of length-classes differed over the year (Fig. 2), with proportionally more large trout (>30 cm) occurring in January–February and more small trout (10–20 cm) in May–June. From July to December, most trout were from 20–30 cm. Very small trout (<10 cm) were not present in the lake but these were observed in confluent streams.

Capture rate in gill nets (number per 12 h set) varied seasonally and spatially (Fig. 3). It was lowest in winter (0.20), increasing during spring and summer reaching the highest (0.80) in autumn. This probably reflects seasonal differences in amount of movement and relative abundance. Capture rate was greatest (0.55) close to shore and lowest (0.21) in the central areas of the lake (>4 m depth), the differences being most pronounced during autumn. Two-factor ANCOVA (season and lake position on capture rate with year as a covariate) indicates significant associations (season $F = 29.6_{DF=3}$, $P > 0.001$, lake position, $F = 9.6_{DF=2}$, $P < 0.002$, interaction, $F = 22.6_{DF=6}$, $P < 0.001$, covariate, $F = 1.5_{DF=1}$, $P = 0.2$).

Numbers of trout captured in the fyke net also varied seasonally and yearly. Catches during late spring and early summer were approximately twice that of winter (Fig. 4). The peak in spring results from increased movement of trout during rising temperatures and the influx of small trout into the lake from surrounding creeks. In contrast, there is a sharp reduction during June which may result from off-shore movement, emigration into adjoining streams, and possible mortality from avian piscivores which are present during this period (Reimchen and Douglas 1984). Summer catch was lowest in 1983 and highest in 1988, indicating recovery of population numbers from the earlier gill-netting period.

Yearly population size of trout was estimated with three methods (Table 1). Average population size overall was 198

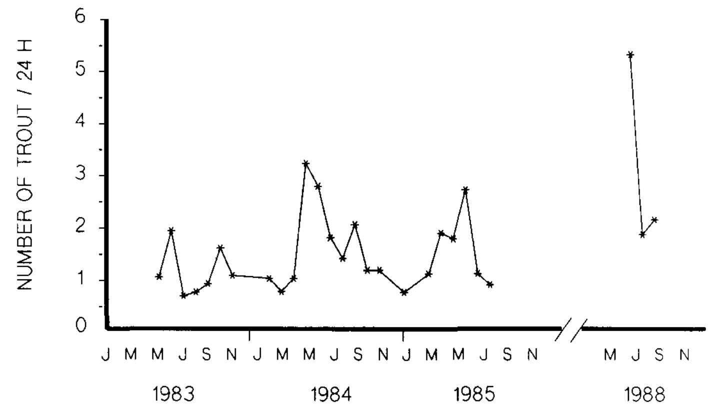

FIG. 4. Number of trout captured in fyke net/24 h. Each data point comprises cumulative effort for 15–31 d/mo.

individuals (Schnabel), 207 (Petersen), and 336 (Jolly-Seber) and with each method, numbers were lowest in 1983 and 1984 following the previous period of gill-netting. Comparisons of estimates in 1988 with those in 1985 yield contradictory trends in population recovery with Petersen producing a reduction in 1988 and Jolly-Seber a population doubling. I consider Petersen's estimates to be most reliable for this investigation. Each estimate is independent of each other and is based on narrow time blocks. As such, these require the fewest assumptions and would be least affected by seasonal differences in mortality, immigration, and emigration.

Seasonal abundance of trout, determined from a series of Petersen's estimates over the year, show lowest numbers in winter and highest in spring and summer (Table 2). Based on a visually smooth-fitted curve, I use the following estimates of trout population sizes in subsequent calculations: Dec./Jan./Feb./Mar. = 115, April = 110, May = 200, June/July = 250, Aug. = 200, Sept. = 100, Oct./Nov. = 90.

Stickleback ranged in size from 7 mm (newly hatched) to 110 mm. Following hatching (from May to August), stickleback achieved a length of 40 mm within 1 yr (0+), 60 mm within 2 yr (1+), 70 mm within 3 yr (2+), and 80 mm within 4 yr (3+). Mean adult size in the population was 80 mm. Individuals can survive for 6–7 yr (T. E. Reimchen, unpubl. data) and consequently the adult cohort was composed of multiple year-classes.

Stomach Analyses of Trout

Overall, 21% of the trout had empty stomachs, most of these occurring from January to April. Stomachs in these winter fish were highly contracted, indicating a lack of foraging, while the occasional summer-captured trout without food had distended stomachs, characteristic of recent digestion rather than a cessation of feeding. Stickleback and invertebrates (primarily winged ants, Hymenoptera, Formicidae) were the dominant food throughout the study period (Fig. 5). Excluding fish with empty stomachs, stickleback occurred in 89.3% of the trout while invertebrates occurred in 21.7%. A comparable pattern occurs with relative volume as stickleback were the major (>80% stomach volume) prey in 85% of the stomachs. Of 1900 fish extracted from the stomachs, 1891 (99.5%) were stickleback and eight were juvenile salmonids. Stickleback were virtually the only prey taken during autumn and winter, but this proportion declined marginally during summer when winged ants comprised the major alternate prey. During this 2-wk

TABLE 1. Population estimates of cutthroat trout at Drizzle Lake. Data from 1988 represents summer only.

Method	1983	1984	1985	1988
Petersen	152(85–260)	128(79–187)	322(197–553)	225(58–563)
Schnabel	160(147–175)	201(178–297)	210(168–270)	220(198–256)
Jolly-Seber		122(48–172)	296(243–348)	589(186–1038)

TABLE 2. Petersen's estimates of cutthroat trout population size at Drizzle Lake. Tagging mark changed for each date.

Number marked (date)	Number caught (date)	Number recaptured	Population size	95% Confidence limits	
48 (5–6/83)	64 (6–8/83)	11	260	130	390
35 (8–9/83)	82 (10–11/83)	23	121	80	162
22 (10/83)	30 (11/83)	7	85	36	134
14 (11/83)	61 (11/83–02/84)	5	145	41	249
66 (2–4/84)	87 (5–7/84)	30	187	134	241
36 (5–6/84	73 (6–7/84)	19	133	84	183
25 (8–9/84)	24 (9–84)	4	125	34	216
40 (9–10/84)	75 (10/84–3/85)	25	117	80	153
11 (11/84)	85 (1–4/85)	11	79	38	119
21 (1–3/85)	86 (4–5/85)	5	305	82	527
20 (4/85)	82 (5–6/85)	2	553	10	1097
35 (5/85)	85 (6/85)	12	232	118	346
35 (6/85)	44 (7–8/85)	7	197	78	316
51 (1/6/88)	60 (3/6/88)	12	239	126	353
	39 (4/6/88)	10	185	94	277
	36 (2/7/88)	11	157	86	229
	22 (4/7/88)	4	235	65	404
	20 (1/8/88)	5	179	64	293
	21 (3/8/88)	3	281	54	507
44 (3/6/88)	39 (4/6/88)	3	440	67	813
	36 (2/7/88)	6	233	84	381
	63 (8/88)	4	563	122	1005
20 (4/6/88)	36 (2/7/88)	3	185	29	341
	63 (8/88)	5	213	60	367
11 (2/7/88)	22 (4/7/88	2	84	6	163
	41 (10/8/88)	7	58	23	92
13 (4/7/88)	21 (3/8/88)	2	95	7	184

period, large rafts of ants floated on the lake following a major annual dispersal from surrounding forests.

Diet was largely independent of size of trout except during summer when small trout had proportionately fewer stickleback in the diet than did larger trout (Fig. 6). Log-linear analyses shows that both size and season contribute unique effects to trout diet (season·diet, length·diet; $P<0.001$ for both interactions).

Number of stickleback per trout stomach ranged from 0 to 55 with a mode at one and a mean of 5.8 (Fig. 7). Bimonthly trends indicate lowest number in spring, increasing values over the summer and highest means in late autumn ($P<0.001$, Kruskal-Wallace test).

Trout consumed stickleback 9–90 mm in length. Size frequency distributions of stickleback eaten differed among seasons (Fig. 8A) and appeared to reflect seasonal variation in size distribution of stickleback available. From September to April, the greatest predation occurred on the 20–40–mm size cohort and there was low but equivalent consumption among each of the larger size-classes.In May/June, there was a broadening of the distribution with similar levels of predation throughout the 20–80 mm range but a moderate mode from 50 to 60 mm. In July/August, distribution was distinctly bimodal, the lower mode (14 mm) comprising young-of-the-year (YOY) recruitment into the population and the second mode (48 mm) corresponding to 1+ year-classes.

Small trout (10–19 cm) took 10–30-mm stickleback with a mode near 20 mm (Fig. 8B). Among progressively larger size-groups of trout, there was a graded increase in average size of stickleback such that among trout >35 cm, modal length of stickleback in the stomachs was about 70 mm. Size relationships between predator and prey were similar during each bimonthly interval although the strength of the relationship is variable (Fig. 9). Correlation coefficients were lowest in summer and highest in autumn and winter. Variability of prey sizes was also associated with predator size since larger trout took a greater size range than did small trout ($P<0.001$, for each bimonthly period, Bartlett's test for homogeneity).

Estimating Total Prey Consumption for the Trout Population

Daily food requirements of trout

Estimates of optimal daily food consumption (maintenance and growth) of salmonids were derived from the following equation (Elliott 1976):

$$[3] \quad Dcal = 15.116 \cdot W^{0.767} \cdot e^{0.138} \cdot T,$$

where $Dcal$ = daily consumption in calories, W = weight of trout (g), and T = water temperature (°C).

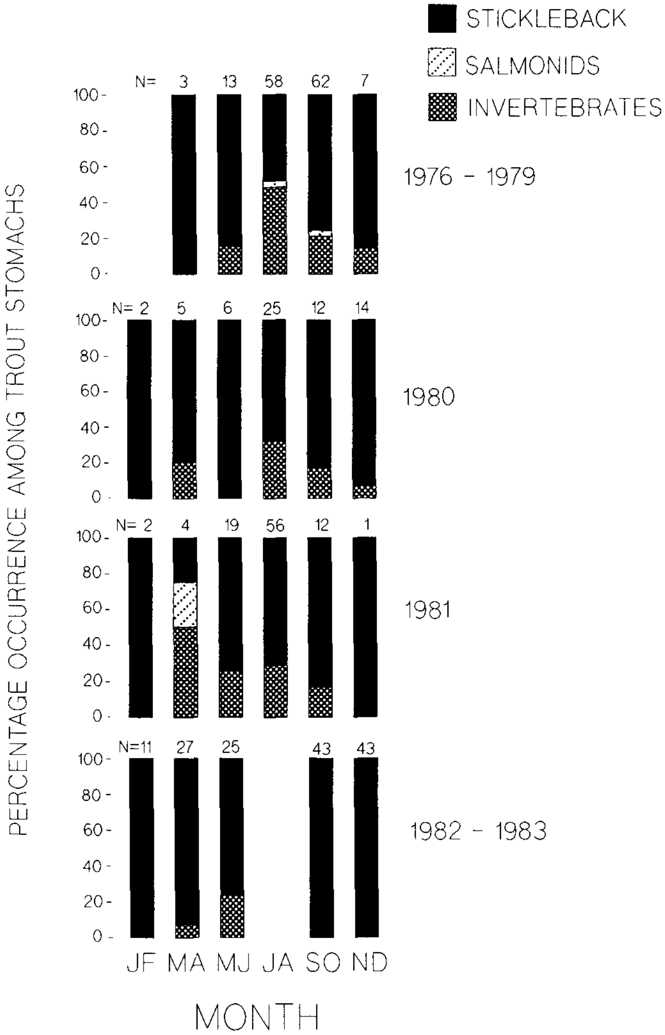

FIG. 5. Bimonthly patterns of trout diet. Vertical axes represent the proportion of trout stomachs containing the item. Proportion of fish with empty stomachs were: 1976–79 = 24%, 1980 = 23%, 1981 = 9%, 1982–83 = 17%.

Assuming an average caloric equivalence of 1.2 kcal/g tissue (Cummi: ; and Wuycheck 1971), caloric consumption can be converted to grams:

[4] $Dg = Dcal \cdot 1.2^{-1}$,

where Dg = daily consumption in grams.

Evaluating the weight of stickleback (Ws) eaten requires several refinements to this estimate since their relative contribution to the trout diet varies both with season (Fig. 5) and with length-class of trout (Fig. 6). For each 1-cm size-class of trout (i), I derived estimates of weight of stickleback eaten per month from the following:

[5] $Ws_i = \Sigma\,[Dg_i \cdot P_i \cdot F \cdot S \cdot M]$,

where Ws_i = weight of stickleback eaten by trout of the ith size class, Dg_i = daily food consumption by trout of the ith size class (from equation [4], P_i = numbers of trout in the population of the ith length-class (from Fig. 2 and Table 3), F = frequency of trout foraging within each bimonthly interval, S = frequency of foraging trout containing stickleback in stomachs, M = number of days per month.

Comparisons between predicted and actual consumption of stickleback

To ascertain whether the calculations give a realistic estimate, I compared the estimated daily stickleback consumption by trout (from equation [5], $Ws \cdot M^{-1}$) with actual weights of stickleback in trout stomachs. Estimated daily consumption was converted to percentage body weight to compensate for differences in trout body weight; this value (ca 2.5%) is relatively constant over the range of trout lengths observed. Stomach contents were partitioned into two groups, one representing the weight of intact stickleback, and the second representing this value in addition to the reconstructed weights of partially digested fish. Complete evacuation of the stomach, which is temperature dependent, is approximately 24–48 h at 17°C and 72–144 h at 5°C (Popova 1967) and therefore one can predict that actual might approximate predicted in summer but be up to six times greater than predicted in winter. The data (Fig. 10) show that actual stickleback consumption (intact + reconstructed) is about 20% lower than the estimated in summer but up to six times higher than the estimated in autumn and winter indicating that my calculated values, which are used in the following estimates of total numbers of individuals eaten, are realistic.

Estimating numbers of stickleback consumed by trout

Number of stickleback eaten per month (Ns) for each length-class of trout can be derived from combining weight of stickleback eaten per month (equation [5] with the length frequency distribution of stickleback in the stomachs. The latter is however dependent on season and trout length (Fig. 8A, B, 9). For each bimonthly interval, I grouped trout into size-classes$_i$ (10–19 cm, 20–24 cm, 25–29 cm, 30–34 cm, 35–41 cm) and tabulated the proportion of each stickleback length group ($_j$) (7–9, 10–14, 15–19, 20–29, 30–39 mm... etc.

[6] $Ns_i = Ws_i \cdot (n_j \cdot w_j)^{-1}$,

where Ns_i = numbers of stickleback eaten per month for the ith size class of trout, Ws_i = total weight of stickleback eaten per month for ith size class of trout (from equation [5]), n_j = frequency of the jth size-class of stickleback in the stomach, w_j = the weight of the jth size-class of stickleback.

Therefore, total stickleback consumption per month (N) for the entire trout population is

[7] $N = \Sigma(Ns_i)$,

where i = 1-cm length-group of trout between 11 and 41 cm.

Weight and number of stickleback eaten

Estimated annual stickleback consumption was 145.4 kg or 308 770 stickleback. Grouping trout into size-classes shows that the intermediate-sized trout (25–29 cm) took the greatest weight of stickleback per year (Table 4). However, small-bodied trout (14–19 cm), which had the lowest yearly weight of stickleback consumption, consumed the greatest number of individuals.

There is a major seasonal component to the total stickleback consumption by trout with 64% of the weight of stickleback taken from June to August and 13% taken from November to March. Comparable values (74 and 6.8%, respectively) occur in number of stickleback eaten (Fig. 11). The peak consumption in summer results predominantly from increased temperatures and the resultant increase in predicted foraging rates.

Partitioning monthly consumption among length-groups of stickleback yields a substantive season–length interaction

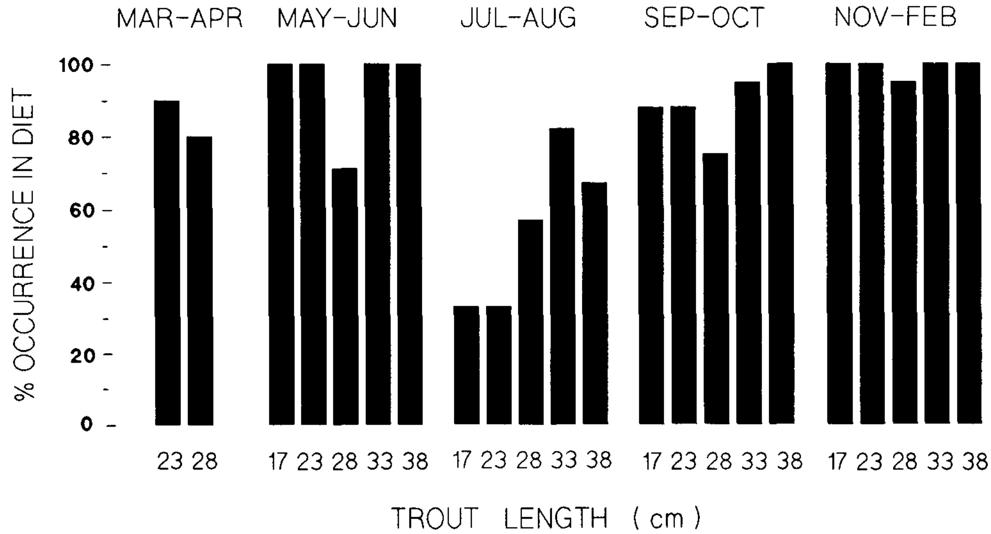

FIG. 6. Proportion of trout stomachs containing stickleback in relation to season and trout length.

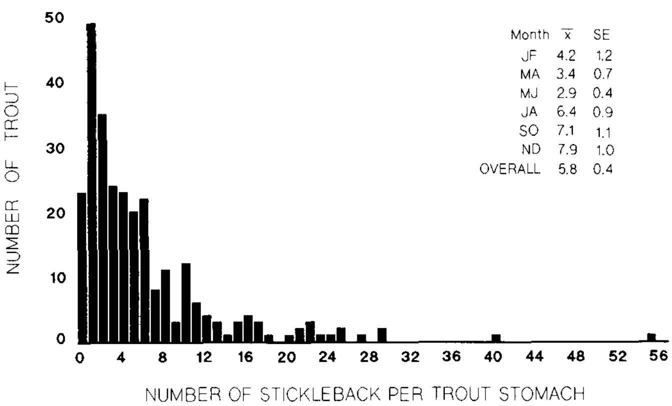

FIG. 7. Number of stickleback per trout stomach. Data from all years included.

(Fig. 12). The smallest length-class (7–20 mm) were taken predominantly in July and August, the only period when this size-group was present. Among the 20–40 mm stickleback, predation took place throughout the year with most occurring from April to October. Among larger stickleback (40–60 mm), there appears to be a contraction of the predation period to summer months. Yet in the largest length-classes (60, 70 and 80 mm), there was a progressive expansion of the predation period to encompass the entire year. The largest fish (>80 mm) are taken commonly in both winter and summer and less frequently in spring and autumn.

Total yearly predation on stickleback, partitioned into length-classes, is shown in Fig. 13A. The smallest fry (7–9 mm) are relatively infrequent in the stomachs while larger fry (10–20 mm) comprise the most common length group and account for 44.7% by number of the total predation. Among progressively larger stickleback, there is a gradual reduction in numbers consumed. Adult stickleback (>70 mm) incur the lowest predation.

Length-classes of eaten stickleback were placed in age-groups to determine age-specific mortality levels (Fig. 13B). The 0–1 year-class comprise 73% of the total predation by trout while the 3+ year-groups represent 2%. There is approximately a 75% reduction (range 67–84%) in consumption in each successive year-class.

General estimates of consumption levels relative to population size are possible. The 240 842 YOY stickleback that were eaten comprise 2.0% of the total number of individuals originally present at the post-hatching stage while total consumption (all age-classes) represent 2.6% of the original cohort. The 3112 adults eaten represent 4.1% of the total adult population in the lake.

Discussion

Previous studies of cutthroat trout indicate a variable diet including benthos, midwater zooplankton, fishes, and surface insects, the proportion of each depending on the size of the trout, the season and the occurrence of competitors (Andrusak and Northcote 1971; Armstrong 1971; Moodie 1972; Sigler et al. 1983; Skinner 1985; Luecke 1986; Loch and Miller 1988). At Drizzle Lake, stickleback are the dominant element in the diet throughout the year except among small trout during summer when insects predominate. The extent of piscivory, which is very high, has previously been observed where cutthroat trout are sympatric with Dolly Varden (Nilsson and Northcote 1981), a species also present in this lake.

Previous studies have shown that stickleback are rare in the diet of small predatory fish (<20 cm) (Frost 1954; Fortunatova 1959), presumably since spiny prey are unsuitable for young predators (Popova 1967). McPhail (1977), working with fish in Vancouver Island populations, indicated that cutthroat trout less than 20 cm rarely ate stickleback. At Drizzle Lake, these prey represented the major diet of small-bodied trout (14–19 cm) throughout most of the year. This is surprising since the stickleback from this population have exceptionally long and robust spines (Moodie and Reimchen 1976). Although juvenile coho salmon (40–60 mm SL) were abundant in the littoral region, these were uncommon in the diet (see also Moodie 1972; Loch and Miller 1988). It is probable that the paucity of suitable alternate prey in this dystrophic lake has resulted in the high consumption of stickleback by small trout and may partially explain why even smaller trout (<12 cm) are rare or absent in the lake.

The prevalence of stickleback and virtual absence of small salmonids in the cutthroat trout diet is characteristic of other piscivores in this locality. Kingfisher (*Ceryle alcyon*), common loon (*Gavia immer*), grebes (*Podiceps* spp.), and river otter

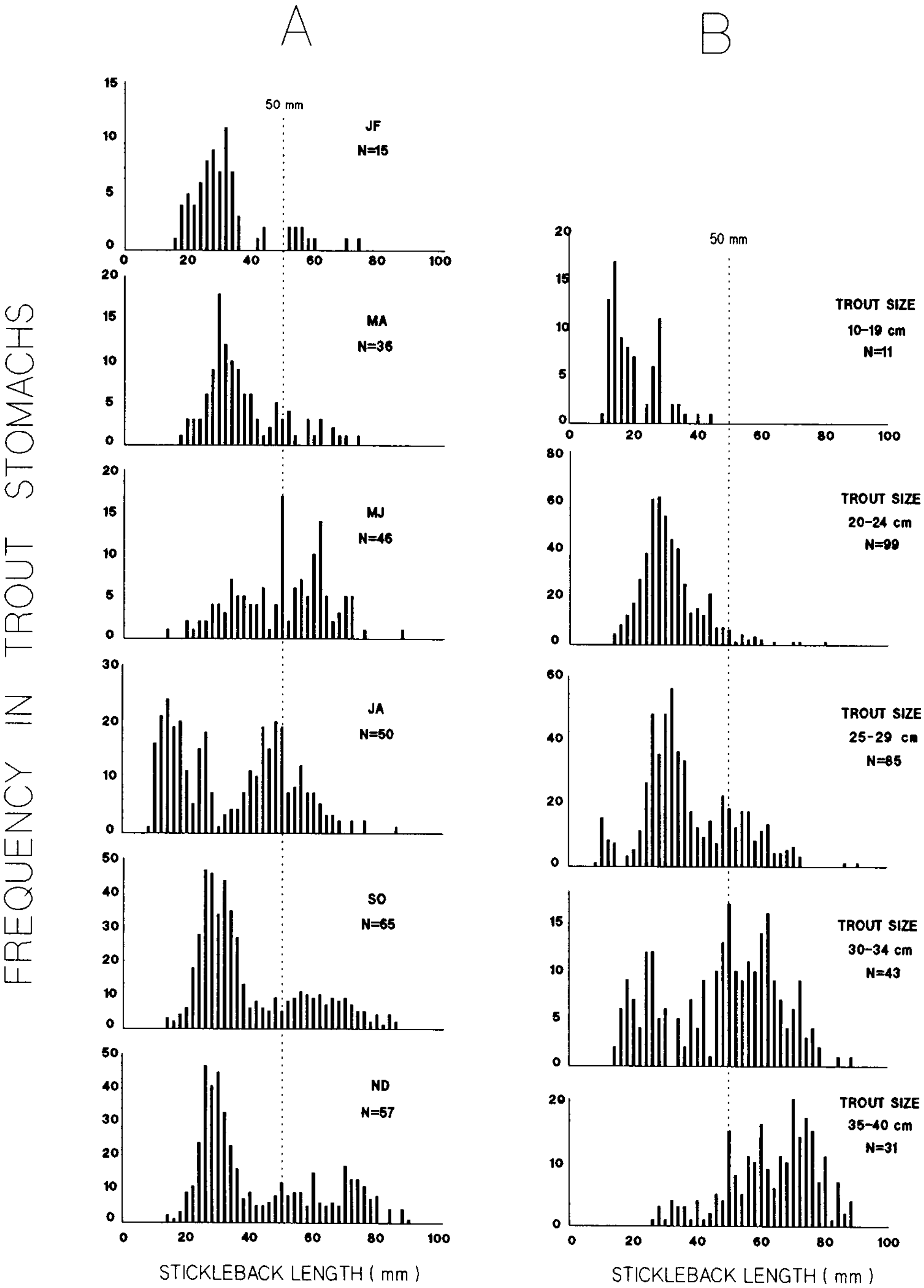

FIG. 8. Standard length of stickleback in trout stomachs at bimonthly intervals (A) and for different size-classes of trout (B). Vertical axes show numbers of stickleback in each millimetre-length-class. N = number of trout stomachs.

(*Lutra canadensis*) also forage primarily (>90% of the diet) on stickleback (Reimchen and Douglas 1984; Reimchen 1990). In northern Europe, stickleback often comprise the major element in the diet of mergansers, terns, and kingfishers (Rad 1980; Sjoberg 1989). Presumably, the small size, slow swimming speed, and abundance make stickleback a preferred prey. Such observations argue for caution in recent suggestions (O'Neill and Hyatt 1987) that number of stickleback be controlled to minimize their effect on juvenile sockeye salmon (*Oncorhynchus nerka*) with which they compete for zooplankton.

Analyses of seasonal predation levels predicted that the overwhelming majority of stickleback would be eaten during summer, primarily as a consequence of the high metabolic requirements. The extent of this major seasonal pulse would be less if, for example, trout moved offshore during summer to colder water (i.e. Andrusak and Northcote 1971) or if daily requirements were increased in winter, for example, during gonad development (Elliott and Persson 1978). Other studies of predation on stickleback (Moodie 1972; Hagen and Gilbertson 1973), have suggested that autumn, winter, and spring may have the greatest predation levels. This conclusion is based on the observation that a greater proportion of trout stomachs contained stickleback and there were greater numbers of stickleback per stomach during these cooler seasons. Both of these trends also occur in the present study. However, in winter tem-

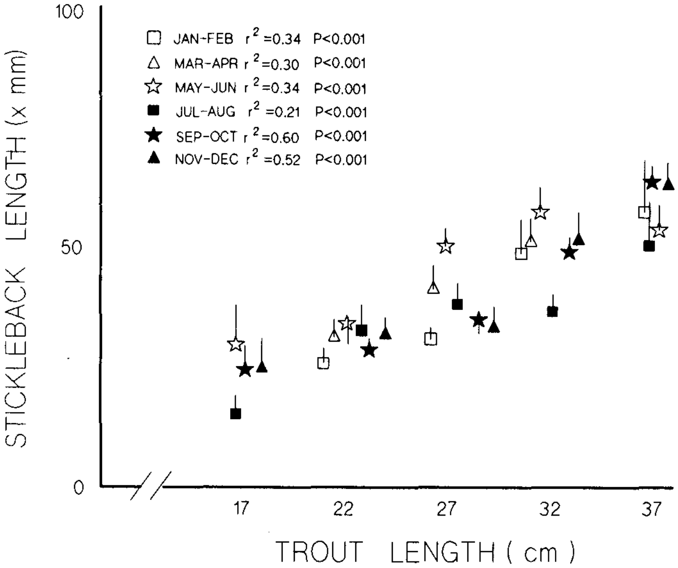

FIG. 9. Mean length (+ 95% confidence limits) of sticklebacks in stomachs in relation to trout size and bimonthly period.

peratures (e.g. near 5°C), stomachs may contain the remains of fish from 4–6 d of foraging while in summer (17–20°C), the entire contents of the stomach can be digested in less than 24 h (Molnar et al. 1967; Popova 1967). Consequently, increased occurrence of prey in autumn and winter may reflect reduced evacuation rates rather than increased predation rates.

Seasonal differences in size-specific mortality are a common feature in size-structured populations since the availability of each size-class of prey will differ over time as a consequence of body growth (Werner and Gilliam 1984 for review). Accordingly, in the Drizzle Lake population, juveniles (<20 mm) are only available during summer following the spring breeding period while large stickleback (>70 mm) are abundant throughout the year and are found in the stomachs in all seasons, particularly summer and winter. This explains part, but not all, of the seasonal variability in consumption levels. Predation on the 40–60-mm size-class appeared to be restricted to summer even though this size-class can be found year-round. One characteristic of this class is that it is primarily limnetic (T. E. Reimchen, pers. observ.). Increased predation would occur if trout, which are primarily littoral foragers, moved offshore during summer. Such movement has been observed in several localities, presumably as a response to rising littoral temperatures (Andrusak and Northcote 1971). Sharp reduction in littoral fyke net captures during July are consistent with this suggestion (Fig. 4). Results from gill nets show that most trout activity in autumn and winter is within 100 m of shore while in spring and summer, it is equally distributed in shoreline and open water regions, consistent with increased limnetic predation levels during these periods.

Total yearly consumption estimates are subject to various errors. For example, organisms differ substantially in their caloric value, from 0.9–1.6 $kcal \cdot g^{-1}$ (Cummins and Wuycheck 1971). I assumed an average food value of 1.2 $kcal \cdot g^{-1}$ since this comprised a mixture of both fish and insects. Increasing this value to 1.35 kcal. g^{-1}, that is, if all the prey were similar in nutrient value to an average fish, would reduce total stickleback consumption by 11%. Any movement of the trout into cooler waters during summer (when 65% of the total yearly predation is predicted), would result in a reduction in metabolic rate and a corresponding reduction in consumption. Lowering average temperature by 3°C throughout the year reduces predicted consumption by 50%. I also computed a range of predation estimates by arbitrarily changing length of trout. A 5-cm reduction in trout length decreases yearly weight consumption of stickleback by 40% but increases numbers by 80%. A 5-cm increase in length (with the resultant loss of the 14–19-cm class) would increase yearly weight of stickleback eaten by 60% but reduce numbers of stickleback eaten by 22% (since fewer small trout are present to eat small stickleback). Small changes in predator size therefore alters the size-specific mortality and potential selective pressures on the prey.

The age-specific predation curve showed a 75% average reduction in consumption of each successive year-class of stickleback. This curve is not substantially different from the survivorship curve assumed to occur in many fish populations. Such a relationship could imply that trout are consuming the same proportion of each age-class in the stickleback population. Many predatory fish are opportunistic and the proportion of taxa in the stomach commonly tracks the abundance of prey (Frost 1954; Popova 1967). However, predatory fish are gape-limited (Popova 1967; Werner 1974; Zaret 1980; Tonn and Paszkowski 1986; Werner and Hall 1988) and therefore, the prey-size consumption curve in size-structured populations will be dependent on the size distribution of the predator (e.g. Nielsen 1980). The reduction in predation levels on the larger size-classes of stickleback probably results from a corresponding reduction in progressively larger trout capable of swallowing the larger stickleback. A 70-mm stickleback with spines erect has a cross-sectional diameter greater than the gape of most trout in the lake and is usually rejected by the trout either during pursuit or during manipulation (T. E. Reimchen, unpubl. data).

Stickleback fry (7–9 mm) are the most abundant length-class in littoral regions during summer yet they represent only 2.6% of the diet. Fry will be digested quickly and would be less detectable in the stomachs but I suspect that this is not a significant factor. While these fry are larger than the minimum

TABLE 3. Values used for calculating total stickleback consumption by cutthroat trout.

	J	F	M	A	M	J	J	A	S	O	N	D
Population estimates of trout (*N*)	115	115	115	110	200	250	250	200	100	90	90	115
Frequency of trout foraging (%)	46	46	47	77	100	100	100	100	100	100	100	100
Temperature °C	4.9	4.9	5.5	7.2	10.5	14.5	16.9	16.9	14.4	10.0	4.5	4.0
Frequency of stickleback in diet (%)												
Trout size = 14–19 cm	100	100	85	85	75	75	75	75	85	85	100	100
20–24 cm	100	100	85	85	86	86	71	71	81	81	100	100
25–29 cm	100	100	95	95	75	75	72	72	84	84	88	88
30–34 cm	100	100	95	95	88	88	74	74	91	91	100	100
35–41 cm	100	100	100	100	100	100	100	100	100	100	100	100

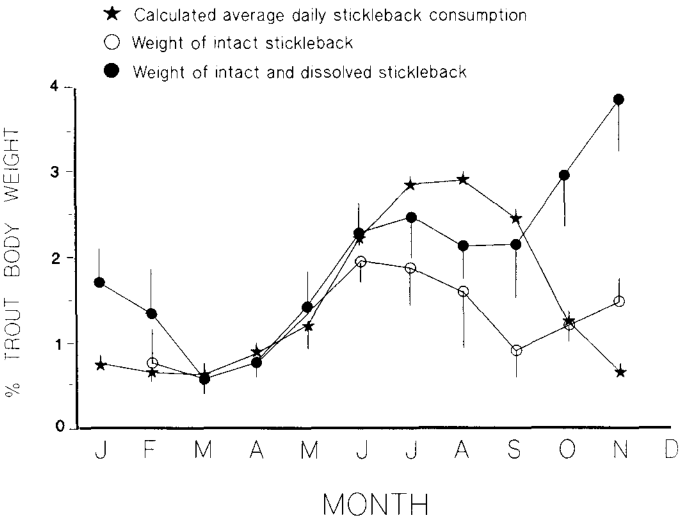

FIG. 10. Mean values (±1 SE) of predicted stickleback consumption in comparison to actual weight of stickleback in trout stomachs. All weights of stickleback converted to percent trout body weight.

TABLE 4. Yearly consumption of stickleback by cutthroat trout at Drizzle Lake.

	Total consumption of stickleback	
Trout size (cm)	Weight (g)	Numbers
14 – 19	10 558	149 504
20 – 24	36 506	72 465
25 – 29	69 984	63 159
30 – 34	21 670	17 723
35 – 41	15 673	5 919
Total	145 391	308 770

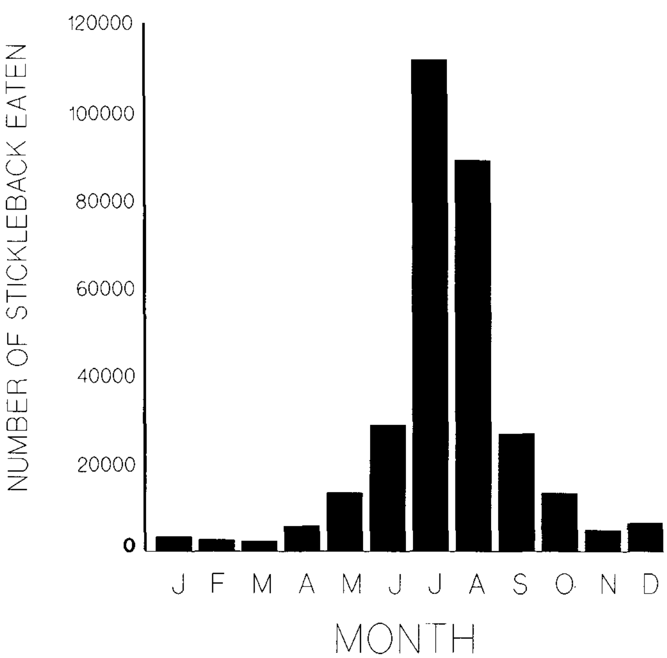

FIG. 11. Monthly consumption of stickleback by trout at Drizzle Lake. Histogram shows average consumption using representative parameters (see Table 3).

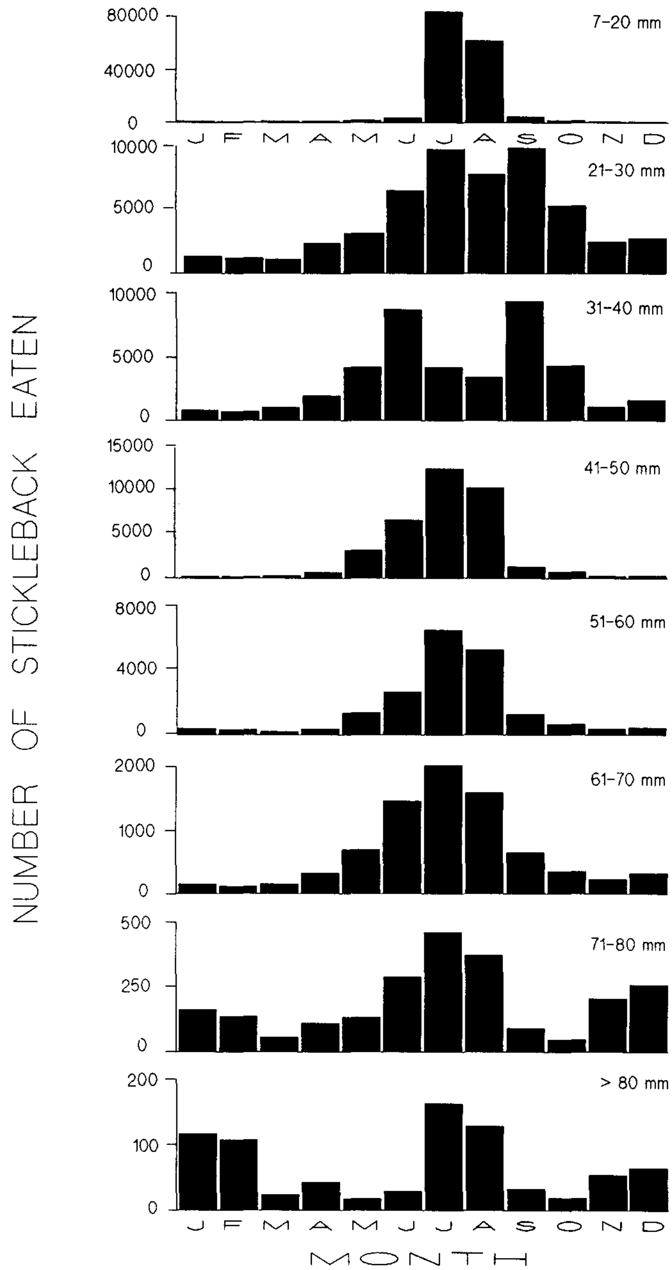

FIG. 12. Size-specific consumption of stickleback at monthly intervals. Vertical axes show absolute number of stickleback eaten. Note differences in scale.

prey size (2–3 mm) (Skinner 1985), they are smaller than the average stickleback (17 mm) observed in small trout during July and August when fry were most abundant. Popova (1978) found that prey of piscivorous fish were generally from 10–40% the body length of the predator. Stickleback fry (9 mm) would be about 5% the body length of a small-bodied trout (17 cm) and therefore potentially outside the preferred prey-size distribution. In addition, fry may be unavailable to these foragers if microhabitats provide refuge (for example, Foster et al. 1988).

Yearly prey consumption by predators relative to total prey population are highly variable within and between species (see Vetter 1988 for review). Lake whitefish (*Coregonus clupeaformis*) had an average natural mortality rate of 49% per year-class (range 18–86%) although it is unknown what proportion of this was from predators (Healey 1975). In Finland, northern pike (*Esox lucius*) consumed about 40% of the older age-classes

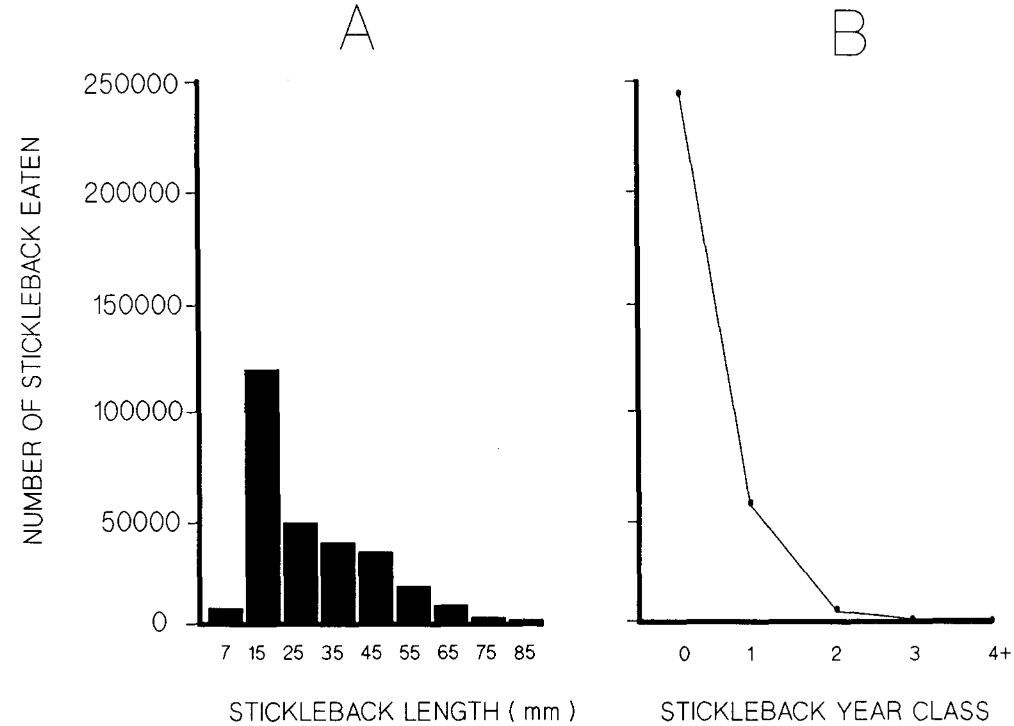

FIG. 13. (A) yearly size-specific (B) age-specific consumption of stickleback at Drizzle Lake from trout predation.

(≥2 yr) of perch (*Perca fluviatilis*) (Rask and Arvola 1985). In the Volga delta, four species of predaceous fish collectively consume about 11% of the 0+ year-class and 1.5% of the 1+ and 2+ year-classes of a population of roach (*Rutilus rutilus*) (Popova 1978). In Paul Lake, British Columbia, rainbow trout (*Oncorhynchus mykiss*) (formerly *Salmo gairdneri*) consume less than 7.5% (possibly as low as 0.15%) of population of redside shiners (*Richardsonius balteatus*) (Crossman 1959). My estimate for trout consumption of the adult stickleback population (4%) is therefore low. This may be the consequence of the relatively large body size of the stickleback. Yet, predation on the sub-adult and the juvenile population was only 2% of the initial maximum potential recruitment. This value could be a substantial underestimate since an unknown proportion of the initial egg and fry recruitment are taken by conspecifics, odonate naiads, and Dolly Varden (Reimchen 1990).

In an earlier study at Drizzle Lake, total fish consumption by 14 species of avian piscivores was estimated at 295–573 $kg \cdot y^{-1}$ (Reimchen and Douglas 1984). Therefore, trout are consuming about 40% of that taken by birds. In a large oligotrophic lake in southern Sweden, predatory fish consumed about twice the weight of fish taken by 12 species of resident avian piscivores (Nilsson and Nilsson 1976). Presumably the proportion taken by each group of predators will differ among localities according to the suitability of the prey, the relative abundance of the piscivores and the characteristics of the habitat. Drizzle Lake is deeply colored with maximum underwater visibility of about 1 m (T. E. Reimchen, pers. observ.) which could favour different foraging techniques to those in clear water habitats.

In summary, the evaluation of stickleback–trout associations in this locality demonstrates that mortality differs with season, with lake position, with predator body size, with prey body size, and with the interactions among these factors. This could be expected in size-structured populations. These data establish a demographic framework from which evolutionary forces can be evaluated and clearly indicate the potential complexity of interactions in this relatively simple aquatic community.

Acknowledgements

S. D. Douglas, D. deLeeuw, J. R. M. Kelso, W. A. MacKay, J. S. Nelson, W. Roberts, D. P. Swain, and W. Tonn provided useful comments on the manuscript. I am grateful to S. D. Douglas for extensive field assistance and discussion during the study and to M. Stock for translation of the two Russian articles. These investigations have been financially supported by the Ecological Reserves Program, Government of British Columbia, and by Natural Sciences and Engineering Research grants to the author and to J. S. Nelson.

References

ANDRUSAK, H., AND T. G. NORTHCOTE. 1971. Segregation between cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. J. Fish Res. Board Can. 28: 1259–1268.

ARMSTRONG, R H. 1971. Age, food and migration of sea-run cutthroat trout, *Salmo clarki*, at Eva Lake, southeastern Alaska. Trans. Am. Fish. Soc. 100: 302–306.

BELL, M. A. 1984. Evolutionary phenetics and genetics: the stickleback, *Gasterosteus aculeatus* and related species, p. 431–528. *In* B. J. Turner [ed.] Evolutionary genetics of fishes. Plenum Publishing Corp., New York, NY.

CROSSMAN, E. J. 1959. A predator–prey interaction in freshwater fish. J. Fish. Res. Board Can. 16: 269–281.

CUMMINS, J. W., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. No. 18.

ELLIOTT, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L) in relation to bodyweight, water temperature and ration size. J. Anim. Ecol. 45: 923–948.

ELLIOTT, J. M., AND L. PERSSON. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991.

ENDLER, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, NJ. 335 p.

FEDER, M. E., AND G. V. LAUDER. 1986. Commentary and conclusion, p. 180–189. *In* M. E. Feder and G. V. Lauder [ed.] Predator–prey relationships. University of Chicago Press, Chicago, IL.

FORTUNATOVA, K. R. 1959. Availability of sticklebacks as food for predatory fish of the Volga delta. Zool. Zh. 38: 1689–1701.

FOSTER, S. A., V. B. GARCIA, AND M. Y. TOWN. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74: 577–585.

FROST, W. E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. 23: 339–360.

FUTUYMA, D. J. 1979. Evolutionary biology. Sinauer Associates, Inc. Sunderland, MA. 565 p.

GROSS, H. P. 1978. Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L. Can. J. Zool. 56: 398–413.

HAGEN, D. W., AND L. G. GILBERTSON. 1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific northwest, America. Evolution 26: 32–51.

1973. Selective predation and the intensity of selection acting upon the lateral plates of threespine sticklebacks. Heredity 30: 273–287.

HEALEY, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427–448.

GILES, N., AND F. A. HUNTINGFORD. 1984. Predation risk and inter-population variation in anti-predator behavior in the three-spined stickleback. *Gasterosteus acuelatus*. Anim. Behav. 32: 264–275.

KRAJINA, V. J., J. B. FOSTER, J. POJAR, AND T. CARSON. 1978. Ecological reserves in British Columbia. Ecological Reserves Unit, Ministry of the Environment, Victoria, B.C. 269 p.

LOCH, J. L., AND D. R. MILLER. 1988. Distribution and diet of sea-run cutthroat trout captured in and adjacent to the Columbia River plume, May–July 1980. Northwest Sci. 62: 41–48.

LUECKE, C. 1986. Ontogenetic changes in feeding habits of juvenile cutthroat trout. Trans. Am. Fish. Soc. 115: 703–710.

MCPHAIL, J. D. 1977. Inherited interpopulation difference in size at first reproduction in threespine stickleback, *Gasterosteus aculeatus* L. Heredity 38: 53–60.

MOLNAR, GY., E. TAMASSY, AND I. TOLG. 1967. The gastric digestion of living, predatory fish, p. 135–149. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, UK.

MOODIE, G. E. E. 1972. Predation, natural selection and adaptation in an usual stickleback. Heredity 28: 155–167.

MOODIE, G. E. E., AND T. E. REIMCHEN. 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. Syst. Zool. 25: 49–61.

NIELSEN, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37: 11–19.

NILSSON, S. G., AND I. NILSSON, 1976. Numbers, food consumption, and fish predation by birds in Lake Mockeln, southern Sweden. Ornis Scand. 7: 61–70.

NILSSON, N.-A., AND T. G. NORTHCOTE. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia Lakes. Can. J. Fish. Aquat. Sci. 38: 1228–1246.

O'NEILL, S. M., AND K. D. HYATT. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake. Can. Spec. Publ. Fish. Aquat. Sci. 96 p.

POPOVA, O. A. 1967. The 'predator–prey' relationship among fishes, p. 359–376. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, U.K. p. 215–249.

1978. The role of predaceous fish in ecosystems, p. 215–249. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. John Wiley and Sons, New York, NY.

RAD, O. 1980. Breeding distribution and habitat selection of Red-breasted Mergansers *Mergus serrator* in fresh water in western Norway. Wildfowl 31: 53–56.

RASK, M., AND L. ARVOLA, 1985. The biomass and production of pike, perch and whitefish in two small lakes in southern Finland. Ann. Zool. Fenn. 22: 129–136.

REIMCHEN, T. E. 1983. Structural relationships between spines and lateral plates in threespine stickleback *Gasterosteus aculeatus*. Evolution 37: 931–946.

1988. Inefficient predators and prey injuries in a population of giant stickleback. Can. J. Zool. 66: 2036–2044.

1989. Loss of nuptial color in threespine sticklebacks *Gasterosteus*. Evolution 43: 450–460.

1990. Predators and evolution in threespine stickleback. *In* M. A. Bell and S. A. Foster [ed.] Evolution of the threespine stickleback. Oxford University Press, England. (In press)

REIMCHEN, T. E., AND S. D. DOUGLAS. 1980. Observations of loons (*Gavia immer* and *G. stellata*) at a bog lake on the Queen Charlotte Islands. Can. Field-Nat. 94: 398–404.

1984. Seasonal and diurnal abundance of aquatic birds on the Drizzle Lake Reserve, Queen Charlotte Islands. Can. Field-Nat. 98: 22–28.

REIMCHEN, T. E., E. M. STINSON, AND J. S. NELSON. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. Can. J. Zool. 63: 2944–2951.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 1–300.

SEBER, G. A. F. 1982. The estimation of animal abundance. Macmillan Publishing Co., New York, N.Y.

SIGLER, W. F., W. T. HELM, P. A. KUCERA, S. VIGG, AND G. W. WORKMAN. 1983. Life history of the Lahontan cutthroat trout, *Salmo clarki henshawi*, in Pyramid Lake, Nevada. Great Basin Nat. 43: 1–29.

SJOBERG, K. 1989. Time-related predator/prey interactions between birds and fish in a northern Swedish river. Oecologia 80: 1–10.

SKINNER, W. D. 1985. Size selection of food by cutthroat trout, *Salmo clarki*, in an Idaho stream. Great Basin Nat. 45: 327–331.

STINSON, E. M. 1982. Threespine sticklebacks (*Gasterosteus aculeatus*) in Drizzle Lake and its inlet, Queen Charlotte Islands: ecological and behavioural relationships and their relevance to reproductive isolation. M.Sc. thesis, Department of Zoology, University of Alberta, Edmonton, Alta. 100 p.

TAYLOR, R. J. 1984. Predation. Chapman and Hall, New York, N.Y. 166 p.

TONN, W. M., AND C. A. PASZKOWSKI. 1986. Size-limited predation, winterkill and organization of *Umbra–Perca* fish assemblages. Can. J. Fish. Aquat. Sci. 43: 194–202.

VETTER, E. F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. 86: 25–43.

WERNER, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31: 1531–1536.

WERNER, E. E., AND J. F. GILLIAM. 1984. The onthogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393–425.

WERNER, E. E., AND D. J. HALL. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352–1366.

WERNER, E. E., G. G. MITTELBACH, D. J. HALL, AND J. F. GILLIAM. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64: 1525–1539.

WOOTTON, R. J. 1984. A functional biology of sticklebacks. University of California Press, Berkeley and Los Angeles. 265 p.

ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT. 187 p.