THE LIFE HISTORY AND TROPHIC RELATIONSHIP OF THE NINESPINE STICKLEBACK, *PUNGITIUS PUNGITIUS*, IN THE APOSTLE ISLANDS AREA OF LAKE SUPERIOR[1]

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ABSTRACT

The ninespine stickleback is an important food of juvenile lake trout in the Apostle Islands area. It is the most numerous fish of the area and is distributed in deep waters during the winter and in shallow waters during the summer. Females grow faster than males, reaching an average total length of 80 mm at age 5. Males live to age 3 and attain an average length of 66 mm. Annulus formation on otoliths is complete by mid-July. Seasonal growth is more than half complete by early August; growth of mature females is delayed until after spawning.

Both sexes mature over a period of 3 yr. Spawning occurs from mid-June to late July. Males apparently do not live as long as females, possibly because of a post-spawning mortality. Egg number is a linear function of fish length, although this relationship is different for fish from two separate areas. Environmental differences between these areas, which may affect spawning time, possibly cause the differences in fecundity. Significant quantities of maturing eggs atrophy just prior to spawning, a phenomenon which changes the fecundity relationship.

Sticklebacks eat a variety of invertebrates, particularly the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Food eaten by the stickleback and slimy sculpin is similar, but the adaptability of both species tends to eliminate serious competition. The lake trout is the only serious predator of stickleback.

Investigations were made by the Bureau of Commercial Fisheries (BCF) on the biology of the fishes of Lake Superior from the early 1960's. These studies have been primarily life history studies on economically valuable species such as the lake trout, *Salvelinus namaycush* (Walbaum), various coregonids, and the smelt, *Osmerus mordax* (Mitchill). Some of the more comprehensive of these include Bailey (1964), Dryer (1963), and Dryer and Beil (1964).

When it became apparent that these fish stocks were being rapidly modified by exotic species, particularly the sea lamprey, *Petromyzon marinus* L., additional emphasis was placed on ecological studies of noncommercial fishes whose life histories are interrelated with the exploited ones. One of these, the ninespine stickleback, occurs in BCF index trawl samples in greater numbers than any other. However, prior to the study presented in this paper, its ecological significance in these waters was largely unknown. This study was designed to investigate the life history of the ninespine stickleback in the Apostle Islands region of Lake Superior and determine the importance of its relationships to the economically important fish species of the area.

The ninespine stickleback is one of the most widely distributed northern fishes, occurring in freshwater, estuarine, and coastal saltwater environments (Bigelow and Schroeder, 1953). It is abundant in cool-water habitats similar to Lake Superior throughout the Northern Hemisphere. In middle western United States, it is found in all the Great Lakes except Lake Erie

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(Hubbs and Lagler, 1958). It has also been taken in inland lakes as far south as northern Indiana (Nelson, 1968a), and Moore and Braem (1965) found small numbers in some Lake Superior tributaries. It is a fish of cool, quiet water (Hubbs and Lagler, 1958), and it is generally abundant wherever it occurs in lakes or seas within its range.

METHODS AND MATERIALS

The data for the present study were collected in 1967-69 in cooperation with the BCF Great Lakes Biological Laboratory, Ann Arbor, Mich.[4]

Experimental sampling operations were conducted aboard the BCF research vessel *Siscowet* in conjunction with sampling by BCF in the Apostle Islands, Lake Superior. The main objectives of the BCF program were to enumerate juvenile lake trout, monitor spawning success, measure the impact of the lamprey on the trout population, and contribute research on the biology of other species in the lake.

One of the main objectives of the ninespine stickleback study was to defiine ecological relationships between the stickleback and other fish, particularly the lake trout. With this objective in mind, and within the limitations of the ongoing BCF program, sampling was essentially confined to seven stations within the Apostle Islands (Figure 1). Five of these stations (12, 24, 44, 75, and 86) were sampled regularly as juvenile trout index trawl stations and yielded data pertinent to questions of species interaction. Comparatively, they supported varying numbers of trout and sticklebacks, and historically they comprised the known lake trout nursery areas within the islands. At present, only stations 75 and 86 support good populations of juvenile trout. The other two stations, 2 and 3, support abundant midsummer stickleback populations and comprise shallow, inshore areas. These two stations were outside the regular BCF trout index sampling routine and required special sampling. Collections from these stations provided data for stickleback age and growth studies and supportive information about distribution and relative abundance.

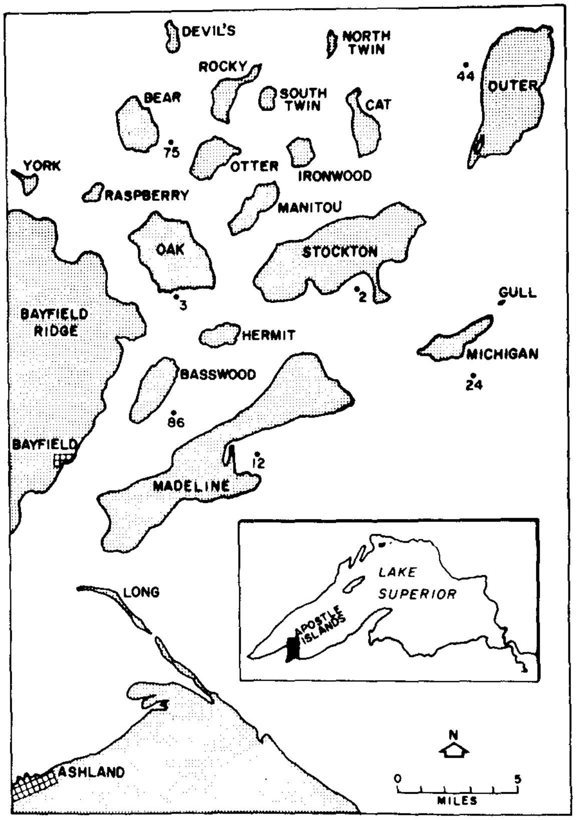

FIGURE 1.—Sampling stations in the Apostle Islands. Blacked out area in inset shows location of these islands in Lake Superior.

A small semi-balloon otter trawl with a 4.7-m headrope, 38.1-mm mesh body (stretched measure), and 12.7-mm mesh cod end was used from a 16-ft aluminum boat with a 40-horsepower outboard motor at stations 2 and 3. A large trawl of the same type (9.4-m headrope, 50.8-mm body, and 12.7-mm cod end) was used aboard the *Siscowet* for deepwater trawling. Adult lake trout were sampled with experimental gill nets ranging from 1.3- to 7.6-cm mesh (bar measure). Zooplankters and sticklebacks examined for stomach contents were collected with a sled-borne plankton net with a 1-m square mouth and 0.158-mm mesh, the bottom edge of which ran approximately 30 cm above the lake bottom. Temperature profiles

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[4] Presently the Great Lakes Fishery Laboratory, U.S. Bureau of Sport Fisheries and Wildlife.

were obtained by bathythermograph at each station.

Trout index trawling aboard *Siscowet* was done for two 2-wk periods annually, one spring and one fall. A total of 286 tows, each 1 mile long, were conducted during the stickleback study from April 1967 through May 1970. Additional records from 322 index tows taken in all ice-free months dating back to April 1965 were also included in the study of distribution. A total of 46 ¼-mile tows were made from June through September, 1968 and 1969, with the small outboard trawl, and 18 tows were made with the sled at various times of the year at the index stations in 1968 and 1969. Trawl samples were separated by species, and the fish were counted. After lake trout were measured, fish samples were put in jars of appropriate size and preserved in 10% Formalin.[5] Samples from the plankton sled were flushed directly into jars and preserved in Formalin.

The main limitation of this sampling scheme was that the index trawl series was conducted at a limited number of stations representing trout nursery areas. It is possible that the biological communities and the resultant ecological interrelationships in these areas may not be representative of the entire Apostle Islands area. Also, since areas of sampling were limited and the efficiency of the index trawl was unknown, it was impossible to estimate absolute biomass of the stickleback population. Alternate methods of population estimation were unfeasible because of the immensity of the population and the area.

Additional methods are discussed in appropriate sections throughout the paper.

DESCRIPTION OF GROWTH

Sticklebacks used for age and growth studies were stratified by length, subsampled if catches were large, and frozen. Otoliths (sagittae) were removed, cleaned, dried in alcohol, cleared in creosote, and mounted on microscope slides in Canada balsam as described by Jones and Hynes (1950). The otoliths contained a series of transparent and opaque rings, and it was evident that the transparent zone was laid down at the beginning of the growing season in late June and early July. Therefore, the annulus was considered the outer edge of the opaque zone. Nomographs, based on the male and female body length-otolith length curves, respectively, were used to calculate body length at each annulus (Carlander and Smith, 1944).

Validation of the Otolith Method

Determination of age from otolith rings was made with little difficulty. In older fish the annulus on the outer margin was not as distinct as in young fish, but usually could be identified at the posterior portion of the otolith. After two independent age determinations of 808 pairs of otoliths, 37 pairs required reexamination because the first two were not in agreement.

Otoliths were analyzed from sticklebacks taken with experimental trawls in 1967 and 1968. The samples represented six year classes and five age-groups. The otoliths were from 372 fish taken at station 2 and 436 taken from station 3. Length-frequency distributions were estimated from 18,175 fish measured from 80 trawl samples.

The following evidence indicates that annuli on otoliths provide an accurate measure of stickleback age and growth:

1. Length distribution by age-group based on otolith readings and modes in length-frequency distribution of all measured fish were in close agreement; however, most distributions exhibited some degree of overlap (Figure 2 and 3). In the June sample (Figure 2), the distribution of age-group 0 fish truncated on the left-hand side because it had been discovered that all of these smaller fish were of 0-group.
2. Calculated lengths at the end of each year of life corresponded well between the various year classes (Tables 1 and 2).
3. There was a general increase in average body length with assigned age of the fish (Tables 3 and 4).
4. The average empirical length of aged fish collected in spring prior to annulus for-

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

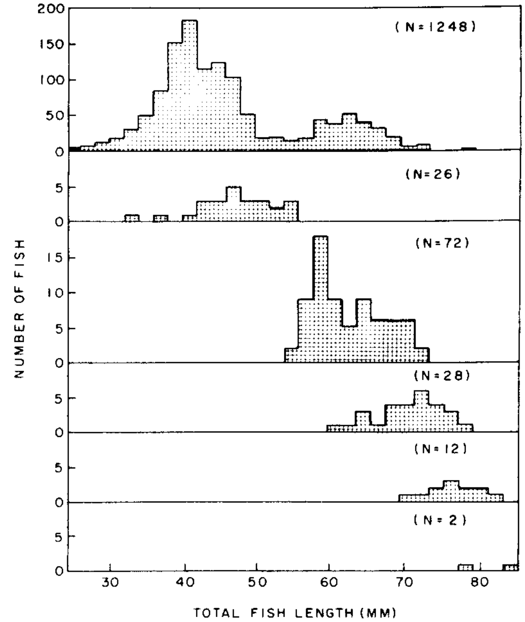

FIGURE 2.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to IV based on otolith readings (lower graphs) of fish collected in June 1967. *N* equals number of fish.

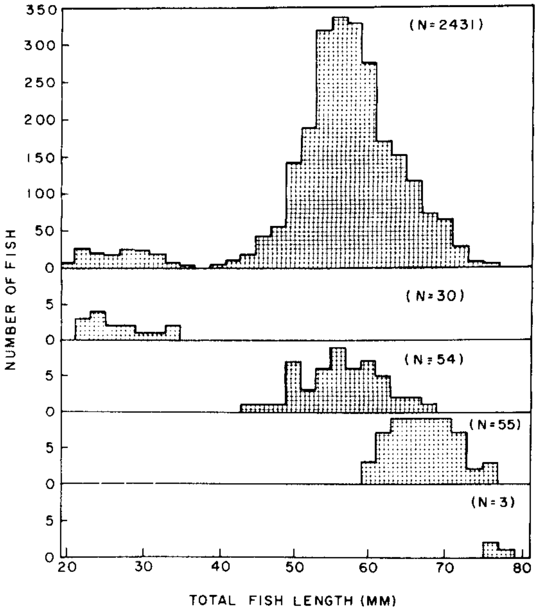

FIGURE 3.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to III based on otolith readings (lower graphs) of fish collected in August 1967. *N* equals number of fish.

TABLE 1.—Average calculated total lengths in millimeters of female ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3	4	5
3	1962	1	45.50	58.75	65.75	74.00	81.00
2	1963	16	46.25	58.25	66.25	73.50	
3	1963	19	48.75	61.53	68.56	76.62	79.00
2	1964	24	44.90	61.20	69.16		
3	1964	40	47.38	61.64	68.79	74.92	
2	1965	60	48.65	61.81	70.50		
3	1965	122	48.66	63.25	70.66		
2	1966	110	47.33	63.22			
3	1966	70	48.47	61.18			
2	1967	24	49.00				
3	1967	2	47.75				
[1]2		234	234	88	23	8	
[1]3		254	254	62	38	9	2
[2]2			47.22	61.87	68.63	73.50	
[2]3			47.75	61.27	68.44	75.18	80.00
Average empirical length of fish in spring prior to annulus formation			47.08	62.32	71.16	77.53	81.00

[1] Total number of fish.
[2] Grand average calculated length.

TABLE 2.—Average calculated total lengths in millimeters of male ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3
3	1963	8	45.21	60.23	66.13
2	1964	8	44.25	59.25	65.50
3	1964	38	43.97	59.73	
2	1965	12	44.25	59.62	
3	1965	70	47.30	60.47	
2	1966	108	49.72	62.70	
3	1966	44	48.54	59.70	
2	1967	10	50.60		
3	1967	22	47.00		
[1]2		138	138	38	8
[1]3		182	182	50	2
[2]2			47.20	60.52	65.50
[2]3			46.40	60.03	66.13
Average empirical length of fish in spring prior to annulus formation			48.55	60.60	67.60

[1] Total number of fish.
[2] Grand average calculated length.

mation agreed closely with grand average back-calculated length of each assigned age-group (Tables 1 and 2). Empirical lengths slightly exceeded calculated lengths, indicating seasonal growth may already have begun.

Table 3.—Length frequency of the age-groups of female sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups				
	I	II	III	iV	V
40-41	5	—	—	—	—
42-43	4	—	—	—	—
44-45	8	—	—	—	—
46-47	10	—	—	—	—
48-49	9	—	—	—	—
50-51	18	—	—	—	—
52-53	6	—	—	—	—
54-55	8	3	—	—	—
56-57	10	9	—	—	—
58-59	7	20	—	—	—
60-61	7	14	—	—	—
62-63	4	13	—	—	—
64-65	4	17	2	—	—
66-67	1	10	1	—	—
68-69	1	17	6	—	—
70-71	—	28	12	1	—
72-73	—	16	16	—	—
74-75	—	6	15	3	—
76-77	—	3	10	2	1
78-79	—	—	7	4	—
80-81	—	1	1	—	2
82-83	—	—	—	1	—
84-85	—	—	—	—	—
86-87	—	—	—	1	—
Average length	52.3	66.5	73.8	76.8	78.5
Number of fish	102	157	70	12	3

Table 4.—Length frequency of the age-groups of male sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups		
	I	II	III
46-47	5	—	—
48-49	1	—	—
50-51	4	—	—
52-53	2	—	—
54-55	11	—	—
56-57	12	—	—
58-59	11	—	—
60-61	7	5	—
62-63	13	5	—
64-65	7	8	1
66-67	4	18	—
68-69	1	8	1
70-71	—	4	4
72-73	—	2	1
74-75	—	4	2
Average length	51.8	66.7	69.4
Number of fish	78	54	9

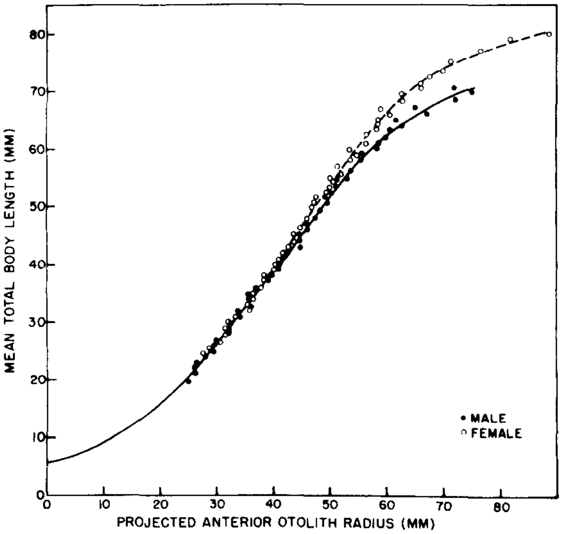

Figure 4.—Body length-otolith length relationship for Apostle Islands ninespine sticklebacks. Solid line, males; dashed line, females.

Growth in Length

The relationship between total fish length and otolith length was estimated from otoliths of 320 males and 488 females. Body lengths at each 1.0-mm interval of otolith length were averaged, and the mean total lengths were plotted against the otolith length. The relationships for fish from stations 2 and 3 were very nearly the same, but the relationship for males and females were empirically quite different (Figure 4). Second degree polynomial regressions were fitted to these data and the resulting equations were:

Males	$Y = -25.864 + 2.146X - 0.011X^2$
Females	$Y = -25.075 + 2.131X - 0.0010X^2$

where Y = total fish length (mm) and
X = projected anterior otolith radius (mm).

Coefficients of determination (r^2) values were 0.978 and 0.958 for male and female equations, respectively. An analysis of covariance showed the elevation was significantly different at the 0.01 level ($F_{1,78} = 48.32$). Therefore, growth parameters were calculated separately for each sex. In Figure 4, the plots were extrapolated to intercept the body-length axis at 6 mm, the length of otolith formation of Alaskan threespine sticklebacks (Jones and Hynes, 1950).

Growth rates were determined for females for the 1962 through 1967 year classes (Table

1) and for males for the 1963 through 1967 year classes (Table 2). Females averaged 47.5, 61.6, 68.5, 74.3, and 80.0 mm in total length at the first through fifth annuli, respectively. Age-groups I, II, and III in males averaged 46.7, 60.2, and 65.6 mm. There was little difference between growth rates of fish from stations 2 and 3. Females from station 2 were longer at the end of 2 of 5 yr of life, and males from station 2 were longer at the end of 2 of 3 yr of life. Females grew faster than males during the first year, being 0.02 and 1.35 mm longer at stations 2 and 3, respectively, at annulus I. These differences increased to almost 3 mm after 3 yr. Females reached age 5, males age 3.

Both sexes showed the greatest growth in length in their first year (Tables 5 and 6), when females attained about 60% and males about 70% of maximum size. The average annual increment calculated from the summation of annual increments was about 30% for both sexes during the second year and on the order of 10% per annum thereafter.

Annulus formation was evident in some sticklebacks as early as June in 1967, and all annulus formation was complete by the second week in July. Annulus formation occurred before spawning and started when surface water temperatures reached about 10°C in 1967 and 1968.

Percentage of annual growth completed at any date during the growing season was computed by comparing the length at capture on a given date in 1967, an average growth year as indicated by average annual increments, with the calculated length at annulus formation in 1968 (Table 7). Male growth was faster at the beginning of the growing season with about 50% of the annual growth being completed by late July. Early seasonal growth of females was slower than in males, and 50% of the annual growth was not complete until mid-August. Growth then declined and was complete or nearly complete in all fish by early December when fall turnover occurred. These calculations are consistent with length-frequency distributions of fish from stations 2 and 3 (Figures 5 and 6). These monthly distributions show that growth, as indicated by increasing modal length of the two apparent age-classes, had begun by July and continued into December.

Older fish had a tendency to grow slower in their first years of life than the younger fish (Tables 1 and 2). This growth pattern (Lee's phenomenon) has been reported for many fish

TABLE 5.—Grand average increment in total length of female ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1962	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	46.25	44.90	48.65	47.33	49.00	47.22	47.22	—
3	1	45.50	48.75	47.38	48.66	48.47	47.75	47.75	47.75	—
2	2	—	—	12.00	16.30	13.16	15.89	14.33	61.55	30.3
3	2	—	13.25	12.78	14.26	14.59	12.71	13.51	61.26	28.2
2	3	—	—	—	8.00	7.96	8.69	8.21	69.76	13.3
3	3	—	—	7.00	7.03	7.15	7.41	7.14	68.40	11.6
2	4	—	—	—	—	7.25	—	7.25	77.01	10.3
3	4	—	—	—	8.25	8.06	6.13	7.48	75.88	10.9
3	5	—	—	—	—	7.00	2.38	4.69	80.57	6.1

TABLE 6.—Grand average increment in total length of male ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	44.25	44.25	49.72	50.60	47.20	47.20	—
3	1	45.21	43.97	47.30	48.54	47.00	46.40	46.40	—
2	2	—	—	15.00	15.37	12.98	14.45	61.65	30.6
3	2	—	15.02	15.76	13.17	11.18	13.78	60.18	29.6
2	3	—	—	—	6.25	—	6.25	67.90	10.1
3	3	—	—	5.90	—	—	5.90	66.08	9.8

TABLE 7.—Percent growth completed at various dates of the 1967 season for ninespine sticklebacks in the Apostle Islands.

Date	Male			Female				
	0	I	II	0	I	II	III	IV
July 22-27		48	75		28	5	37	75
August 8-19	62	69	98	64	54	27	60	
December 4	100	100	100	100	97	79	85	100

species (Lee, 1912). In the Lake Superior study, there appeared to be no significant disappearance of faster growing individuals from the length-frequency distributions (Figures 5 and 6). However, as will be shown below, there does appear to be a sex-specific mortality associated with spawning. Since faster growing males tend to spawn at an earlier age, slower growing males may be left in the population longer. This tendency does not explain the presence of "Lee's phenomenon" among females, where it is most prevalent. Figures 5 and 6 demonstrate that young-of-the-year fish were being sampled throughout the latter part of each season. Therefore, it is possible that biased sampling of precocious individuals in the younger age-groups creates the appearance that younger fish of both sexes are growing more rapidly than older fish did at the same age. To minimize these suspected biases in the growth-rate calculations, back calculations for each year class over successive collection years were averaged as unweighted means.

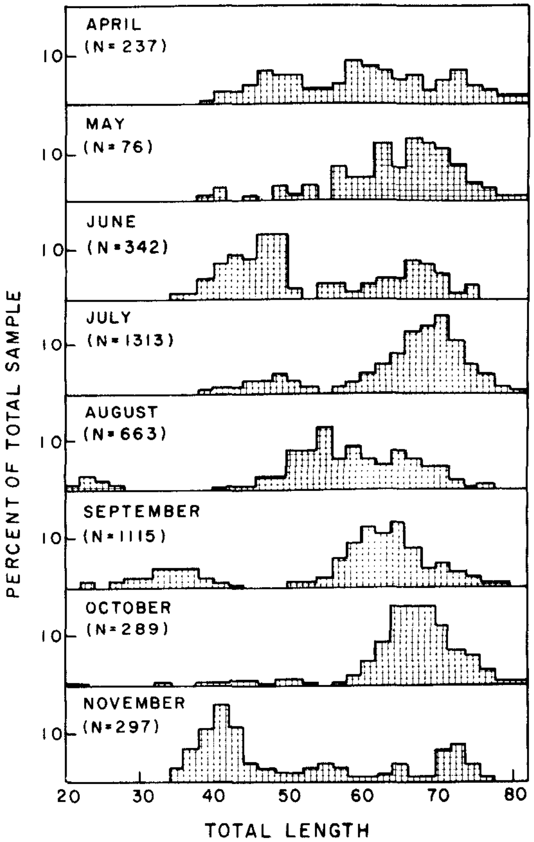

FIGURE 5.—Length-frequency histograms of station 2 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

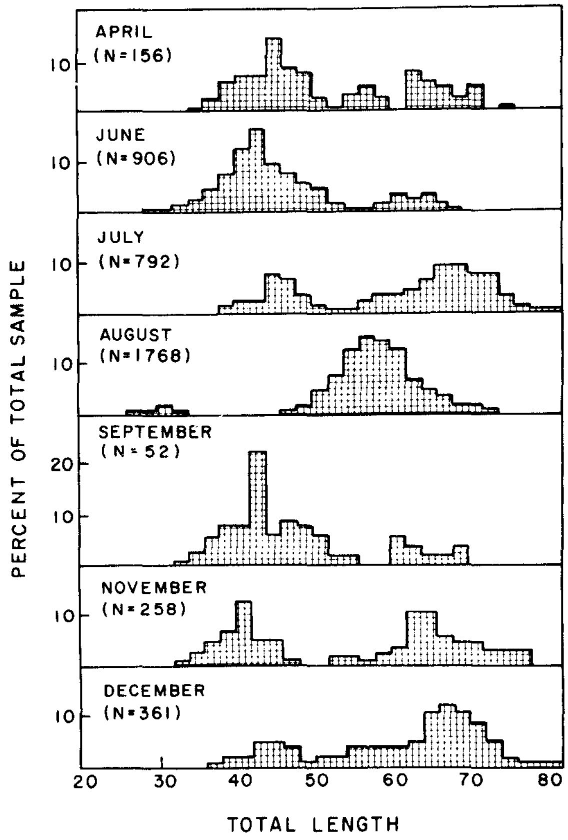

FIGURE 6.—Length-frequency histograms of station 3 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

Growth was fairly stable from year to year (Tables 5 and 6) with the exception of 1964. No explanation for this poor growth year was discovered.

Ninespine sticklebacks from Lake Superior grow as large, or larger, than those reported in other areas. The most comprehensive growth calculations on the ninespine stickleback prior to this study was done by Jones and Hynes (1950) on a population in a small English stream. They found fish reached only 37 mm in 1 yr and 46 mm in 3 yr. The largest fish recorded was 55 mm. These fish were in direct competition with a population of threespine sticklebacks. Nelson (1968b) found the largest fish in a northern Indiana lake to be 67.3 mm. Bertin (1925) and Leiner (1934) both record European ninespine sticklebacks over 80 mm, but Blegvad (1917) found none over 50 mm in Danish brackish waters. McKenzie and Keenleyside (1970) report fish up to 75 mm in Lake Huron. The formula, TL = 1.14SL, was calculated from 300 Lake Superior fish and used to convert reported SL (standard length) to TL (total length) for these comparisons.

Walford (1946) proposed a transformation of growth data to be expressed as a straight line described by the equation:

$$L_{t+1} = L_\infty (1\text{-}K) + KL_t,$$

where L_{t+1} = body length at age $t+1$

L_t = body length at age t

L_∞ = ultimate length

K = slope.

The ultimate length is found graphically where the Walford line intersects a line drawn at 45° through the origin of the graph and is theoretically the greatest length a fish of the population will attain. The slope of the line, K, indicates the decrease in growth rate.

Walford lines were plotted for Apostle Islands sticklebacks from stations 2 and 3 (Figure 7). Means of stations 2 and 3 grand average calculated lengths at each annulus were used to combine station data for each sex.

Calculated values were:

Males	K	=	0.411
	L_∞	=	69.690
Females	K	=	0.672
	L_∞	=	87.660

The ultimate length for males is less than expected from what is known about male length frequency (Table 4). This is probably due to the small number of points used because of the short life span. More points can be included for the female relationship, and the ultimate length is reasonable.

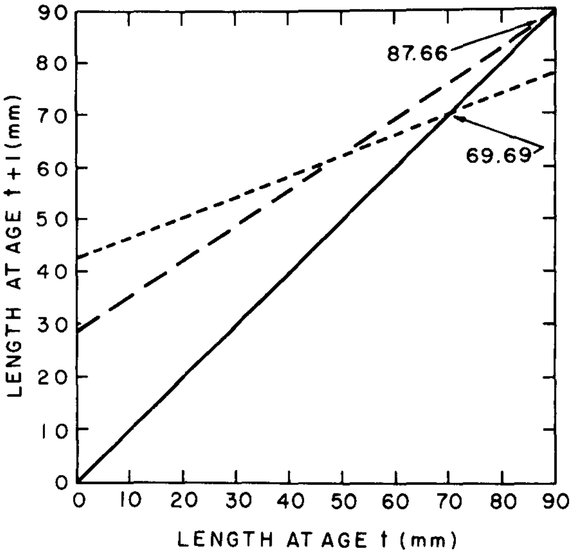

FIGURE 7.—Walford lines for Apostle Islands ninespine sticklebacks. Short dashed line, males; long dashed line, females.

Growth in Weight

Plots of weight against length were made for males and females by calculating average weights for fish at 1-mm intervals. Weights for females in the mature size range were less than male weights. The cause for this was the abrupt drop in weight of females which had just spawned, since the mature female gonad accounts for up to 10% of total fish weight. After females collected in late June and July were omitted from the length-weight plots, the lines for males and females appeared similar.

Analysis of covariance showed slope, and intercept differences were nonsignificant at the 0.05 level ($F_{1,745} = 2.71$ and $F_{1,746} = 1.36$, respectively), and the data were pooled to calculate a length-weight relationship. The resultant regression included 748 fish and was described by the formula:

$$\log W = -4.5681 + 3.2190 \log L$$

where $\log W$ = common log of the weight (0.1g)
and $\log L$ = common log of the length (mm).

Growth in weight was calculated on the basis of weight at the time of each annulus formation (Table 8). The greatest increment in weight occurred in the second year of life for both sexes at both stations. After the second year, growth in weight declined rapidly, but the decline was more pronounced in males.

Instantaneous rates of growth in weight between consecutive ages varied from 0.804 to 0.223 for males and from 0.842 to 0.192 for females.

TABLE 8.—Calculated weight attained by Apostle Islands sticklebacks at the time of annulus formation.

	Male			Female		
Age-group	Total length (mm)	Calculated weight (g)	Percentage increment	Total length (mm)	Calculated weight (g)	Percentage increment
Station 2						
I	47.20	0.662	—	47.22	0.663	—
II	60.52	1.470	122.0	61.87	1.580	138.3
III	65.50	1.821	23.9	68.63	2.215	40.2
IV	—	—	—	73.50	2.751	24.2
Station 3						
I	46.60	0.627	—	47.75	0.687	—
II	60.03	1.401	123.4	61.27	1.494	117.4
III	66.13	1.955	39.5	68.44	2.185	46.2
IV	—	—	—	75.18	2.955	35.2
V	—	—	—	80.00	3.624	22.6

DISTRIBUTION

While some species of sticklebacks can be found in a marine environment far from shore, the ninespine stickleback is an inshore species (Bigelow and Schroeder, 1953). Hubbs and Lagler (1958) state that the species is abundant in the Isle Royale and Keewenaw Bay areas of Lake Superior. BCF operations found sticklebacks in Nipigon Bay, on the north shore of the lake. While sticklebacks were found throughout the Apostle Islands, it should not be concluded that these fish are similarly abundant on all Lake Superior shorelines. Anderson (1969) recovered only 0.1 stickleback per trawl tow in 90 tows in the Duluth area, sampling during all ice-free months. Degradation of water quality may well be the explanation for this; however, no historical records of stickleback abundance in the Duluth area are available to help justify this hypothesis.

Temperature profiles were secured concurrently with trawl tows. Sticklebacks were found in the warmer deep water in early spring, but were evenly distributed at all depths during spring turnover (Table 9). In midsummer they congregated on the warm shallow snoals where water temperatures reached as high as 20°C. When the fall turnover occurred in September, they were again fairly evenly distributed at all depths. By November the fish were beginning to congregate in the deeper water and were found there in great numbers during December. No data are available for midwinter, but it is assumed the deepwater habitat is used at this time since they were abundant there the following spring. Nelson (1968b) also noted sum-

TABLE 9.—Average numbers of sticklebacks caught per 30-min trawl tow each month at various depths during 1967-69.

[Numbers of tows are in parentheses.]

Depth (fathoms)	Apr.	May	June	July	Aug.	Sept.	Nov.	Dec.
3-9	0.0 (2)	2.7 (4)	12.8 (6)	615.7 (16)	641.5 (12)	75.4 (5)	0.3 (5)	
10-26	0.3 (15)	8.4 (11)	14.8 (45)	10.5 (17)	11.4 (16)	80.0 (42)	18.2 (15)	
27-50	58.4 (12)	11.7 (3)	32.7 (16)	0.1 (6)	0.0 (1)	147.1 (9)	114.7 (11)	267.3 (4)

mer inshore migrations of ninespine sticklebacks in Crooked Lake, Ind.

The shoal areas where sticklebacks concentrated in the summer were represented by stations 2 and 3 (Figure 1). Station 2 included a sandy beach, approximately 2 miles long, at Presque Isle Bay, Stockton Island, which gradually deepened and merged with the soft bottom muds of the deeper areas. In summer sticklebacks congregated in large numbers on the beach in ½ to 2 fathoms of water. The fish could easily be seen by eye and were evenly distributed over the bottom throughout the entire beach area. Station 3, along the south shore of Oak Island, was characterized by a sandy shelf about ¼ mile wide paralleling the shore which gradually deepened to 8 fathoms. The bottom then dropped steeply to 12 fathoms. This steep slope was covered with a dense growth of *Nitella* sp. The summer concentration of sticklebacks occurred in this vegetation. No fish could be seen over the sandy shelf, and no fish were caught unless the net was recovered with mats of *Nitella* sp. clinging to it.

Dryer (1966), Anderson and Smith (1971), and field observations by the senior author of this paper indicate that smelt, slimy sculpins, lake trout under 28-cm TL, and trout-perch, *Percopsis omiscomaycus* (Walbaum), had food habits similar to the stickleback and were apparently abundant enough to be potential competitors with the stickleback. Rank correlation coefficients (r_s) were obtained between the average number of sticklebacks caught per 1-mile trawl tow (CPE) and the CPE of these potential competitors in 100 trout index tows. The CPE's were ranked for each species, ties being given the mean rank, and r_s values were determined by the formula presented by Snedecor (1956). The 100 tows were randomly selected from all (322) trout index tows made at stations 86, 75, 44, 24, and 12 from 1965 to 1968. The significant relationships were those for juvenile smelt, trout-perch, and slimy sculpins (Table 10). Sticklebacks inhabited different areas than juvenile smelt and trout-perch, and sticklebacks and sculpins inhabited the same areas, at least during spring and fall. The results of the correlations do not preclude significant relationships at other times of the year or other places, nor do they consider possible effects of differences in availability to the gear. Further discussion of these correlations will be presented in the section on food habits.

TABLE 10.—Rank correlation coefficients (r_s) between stickleback CPE and CPE's of other species in 100 randomly selected index trawl tows in the Apostle Islands, 1965-68.

Species	r_s
Juvenile lake trout to 11 inches	−0.077
Smelt adults	+0.073
Smelt juveniles	−0.461**
Slimy sculpin	+0.568**
Trout-perch	−0.360**

**Significant at 0.01 level (98 degrees of freedom).

RELATIVE ABUNDANCE

Dryer (1966) reported that the ninespine stickleback was the most abundant species in 578 Apostle Islands experimental trawl tows from 1958 through 1963. The average CPE of stickleback during this period was 51.8. Smelt ranked second (CPE = 40.4), and slimy sculpin, *Cottus cognatus* Richardson, were third (CPE = 22.3). Lake trout CPE was 6.8.

Over the 1965-68 period, 322 trout index tows were made, and the relative rank of sticklebacks, smelt, and slimy sculpins was unchanged from the 1958-63 period (Table 11). The CPE's were 61.1, 50.3, and 17.7, respectively. The catch statistics of the two time periods show slight increases for sticklebacks, smelt, and lake trout. Further comparison is meaningless however, because sampling allocations between index stations used in the two time periods were not identical, and extreme between-tow variation was observed. Table 11 does not include data from stations 2 and 3 because they were not used by BCF as trout index trawl stations.

To sample the shallow inshore area of station 2, where sticklebacks congregated in midsummer, ¼ mile tows were made with the small outboard trawl. The wingspread opening of the trawl was determined by measuring the width of the trawl path on the bottom as indicated by ground-rope disturbance immediately after the

TABLE 11.—Average catch per 1-mile trawl tow (CPE) at various index stations in the Apostle Islands calculated from Bureau of Commercial Fisheries index trawling data, 1965 through 1968.

Species[1]	Station 86	75	24	12	44	Weighted mean
Number of tows	99	98	28	76	21	
Stickleback	42.13	93.22	53.52	60.01	4.69	61.11
Smelt	88.44	19.87	20.71	52.33	7.90	50.30
Lake trout	23.16	7.63	4.29	4.63	.76	10.71
Slimy sculpin	7.93	19.63	38.43	20.01	18.57	17.71
Fourhorn sculpin	.38	.72	.36	4.20	1.14	2.00
Spoonhead sculpin	.35	.47	.61	3.29	.14	1.06
Mottled sculpin	.04	.01	—	—	—	.01
Lake whitefish	.76	1.06	.14	.12	3.62	.81
Bloater	4.44	5.38	—	7.30	.33	4.63
Shortjaw cisco	.08	.06	—	.18	—	.08
Kiyi	.01	.01	—	—	—	<.01
Lake herring	.12	.05	—	.14	—	.08
Unidentified coregonid	5.80	.56	—	1.37	1.24	2.30
Round whitefish	1.00	—	13.93	—	13.33	2.03
Pygmy whitefish	.28	.71	.25	1.24	.86	.65
Alewife	.01	.04	—	—	—	.01
Trout-perch	3.08	1.02	.11	.17	7.28	1.69
Burbot	.17	1.03	.43	.45	.10	.50
Longnose sucker	.07	.14	—	—	—	.06
Johnny darter	.01	—	—	—	—	<.01

[1] Taken from: Bailey, R. M. (chairman). 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc., Spec. Publ. 6, 149 p.

trawl was towed through the area. This allowed estimation of minimum density.

Catches with this trawl were highly variable even though visual sightings, during both day and night, indicated fish were quite evenly distributed. Light obviously influenced catch because no fish were caught during the daylight hours even though they could be seen. Moonlight intensity probably influenced the catch, as did wind direction and intensity, by adversely affecting the efficiency of the sampling operation. It is entirely possible these factors also influenced catches by *Siscowet* in deeper waters.

Summer nighttime trawl tows on the sandy beach, station 2, usually caught from 300 to 2,500 sticklebacks in ¼ mile (Table 12). These values correspond to minimum density estimates of 0.18 to 1.49 fish per square meter. Sticklebacks were the only species caught in the area during their summer concentration, but johnny darters, *Etheostoma nigrum* Rafinesque, pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), trout-perch, and smelt were found there in spring and fall.

TABLE 12.—Catches of sticklebacks in 1967 and 1968 on the sand beach of station 2 during the night using the 4.7-m otter trawl and outboard.

Month	Number of tows	Total sticklebacks	Average per tow
April	5	6	1.2
June	3	217	72.3
July	10	6,985	698.5
August	8	7,564	945.5
September	4	3,622	905.4
November	4	0	0.0

REPRODUCTION

Maturation

The gonads of 401 spring-collected fish from which otoliths were extracted were analyzed for maturity. In addition, 34 male and 72 female I annulus fish (determined from length-frequency histograms) were included in maturity studies.

Both male and female sticklebacks matured over 3 yr (Table 13). A greater percentage of males matured at age 1, with large size being a prerequisite for early maturity. By age 2, nearly all fish of each sex were sexually mature, but neither sex was 100% mature until the third year of life. Jones and Hynes (1950) found 99% of a sample of European ninespine sticklebacks mature with 2 yr.

TABLE 13.—Percent of Apostle Islands sticklebacks mature at each annulus with total number of fish in each group in parentheses.

	I's under 50 mm	I's 50 mm and over	II	III	IV	V
Male	34 (56)	56 (40)	93 (78)	100 (10)		
Female	5 (89)	35 (67)	97 (106)	100 (44)	100 (15)	100 (2)

Within the ovaries, several developmental groups of ova can be distinguished. The ovaries were classified into the following stages for maturity:

Immature (I)

Preserved in Formalin, the ova was translucent, spherical, and invisible to the naked eye. Ova of this group are present in the ovaries throughout the year. Ovaries in this stage are slender, elongate, white organs.

Intermediate (II)

The first yolk granules appear in this stage giving the ovary a pale yellowish tinge while making the ova visible without magnification.

Maturing (III)

The yolk granules appear as highly refractive, spherical bodies in the cytoplasm, and ova become opaque. The ovary becomes turgid and deep yellow in color, with ova readily visible but firmly embedded in the follicles. The size of ova in this stage varies widely.

Ripe (IV)

When the ova are about ready to be spawned, a single conspicuous golden oil globule appears in the yolk. The ova readily break from the follicles in which they were formed and flow freely from the oviduct when the sides of the fish are pressed. In Formalin-preserved fish, mature ova can readily be separated from ovarian tissue with a dissecting needle, a procedure which was almost impossible in Stage III fish. The fish is very rotund.

Partly spent (V)

Partly spent fish contained ripe ova but not the full complement. The ova are congregated in the anterior ends of the ovaries, with the posterior portion somewhat flaccid and lighter in color.

Spent (VI)

Ovaries were gradually resuming the appearance of those in the intermediate stage. Ova maturing for the next reproductive period are already visible to the naked eye. Following spawning, resorbing ova remnants were sometimes found.

Female fish were judged to be sexually mature when their ovaries contained ova in developmental Stage II or beyond. Male maturity was established by noting the presence of breeding color, an ink-black patch on the ventral surface as noted by McKenzie and Keenleyside (1970), remnants of which were detectable through the year after its original appearance.

Time of Spawning

The first spent females were observed on June 6 with no great increase in percentage frequency of occurrence until mid-July. By the end of July, all but one of 38 fish were spent, and that one was partly spent. It appears that the spawning season for these fish is approximately 8 wk long. Equally long spawning periods are reported by Nelson (1968b) and Bigelow and Schroeder (1953).

Spawning Habitat

The spawning act was not observed in the lake, therefore the exact location and spawning substrate cannot be identified. McKenzie and Keenleyside (1970) saw Lake Huron *Pungitius* spawning among rocks around the shore. No such activity was noted in superficial observation in the Apostle Islands. Ripe station 3 females and males displaying vivid reproductive coloration were found exclusively in the dense growth of *Nitella* sp. At station 2, ripe fish of both sexes were collected over highly organic muds 12 to 24 fathoms deep, and Lake Superior *Pungitius* spawned successfully in this mud in the laboratory while no spawning resulted in rocky or sandy substrates (Griswold and Smith, 1972).

Fecundity and Egg Size

On 27 June 1969, stickleback samples at station 2 and 3 contained a large proportion of females which were in Stage IV of maturity. These fish were used in the analysis of fecundity. A total of 72 fish were examined from station 2 and 60 from station 3 (Table 14).

Several authors have found a high percentage of atresia in maturing eggs of a number of species. This may cause an overestimate of fecundity (Wagner and Cooper, 1963; Vladykov, 1956; Wydoskii and Cooper, 1966). To determine if appreciable atresia occurred in stickleback eggs, the number of eggs in the 132 ripe fish were compared to egg numbers in fish taken from the same stations about 3 wk prior to spawning (Table 15). Analysis of covariance (Snedecor, 1956) revealed egg numbers in the "green" fish were significantly greater (0.01 level) than those in corresponding size of ripe fish ($F_{1,29} = 7.67$). It appears atresia occurs in maturing ninespine stickleback eggs just prior to spawning. Eggs which appeared to be degenerating after some maturation were almost always present in maturing ovaries. The decrease in egg number at each length interval presented in Table 15 ranged from 24 to 39%. The amount of atresia was not dependent on fish size. Vladykov (1956) estimated atresia affected up to 60% of maturing eggs in natural brook trout populations. It is generally agreed that atresia is a physical reaction to the pressure caused by the growing ovary (Vladykov, 1956).

TABLE 14.—Average number of eggs counted from 132 ninespine sticklebacks of various lengths collected 27 June 1969.

	Station 2			Station 3		
Length (mm)	Mean number eggs	Mean fish weight (g)	Number of fish	Mean number eggs	Mean fish weight (g)	Number of fish
55	—	—	0	84.0	1.217	1
56	—	—	0	—	—	0
57	—	—	0	—	—	0
58	—	—	0	65.0	1.407	1
59	—	—	0	75.0	1.453	1
60	—	—	0	—	—	0
61	—	—	0	—	—	0
62	—	—	0	61.0	1.662	1
63	86.0	1.844	2	59.5	1.737	2
64	—	—	0	68.0	1.712	1
65	74.3	1.827	3	77.7	2.013	6
66	76.0	1.896	3	69.8	1.901	4
67	78.8	1.997	10	71.0	2.101	4
68	82.7	2.031	6	73.0	2.206	4
69	76.8	1.961	5	78.3	2.288	6
70	86.6	2.142	5	87.7	2.371	7
71	82.8	2.254	4	71.3	2.544	3
72	93.4	2.429	7	104.0	2.452	2
73	103.2	2.639	5	82.6	2.766	5
74	98.3	2.400	3	90.0	2.730	7
75	88.0	2.742	5	85.5	2.920	2
76	113.8	2.942	7	94.0	2.776	1
77	112.3	2.990	3	—	—	0
78	95.7	3.070	3	—	—	0
79	—	—	0	103.0	2.962	1
80	103.0	3.010	1	—	—	0
81	—	—	0	98.0	3.522	1

TABLE 15.—Comparison of mean number of eggs per female in fish taken in early June 1970 about 3 wk prior to spawning and fish which were in "running-ripe" condition.

Fish length (mm)	"Green" fish	"Running-ripe" fish
58	—	65.00
59	—	—
60	—	—
61	82.00	—
62	88.50	61.00
63	99.00	72.75
64	98.66	68.00
65	99.62	76.56
66	99.33	72.45
67	116.80	76.57
68	114.50	78.82
69	114.66	77.61
70	114.00	87.24
71	124.25	77.87
72	137.75	95.75
73	126.00	94.70
74	130.66	92.49
75	128.00	87.28
76	132.00	111.32
77	—	112.30
78	158.00	95.70
79	—	103.00
80	—	103.00
81	—	98.00
Total fish	58	132

When means of ripe egg numbers at each millimeter body length interval were plotted for stations 2 and 3 ninespine sticklebacks, linear relationships were implied (Figure 8). Least squares equations which describe the lines were:

$$\text{Station 2} \quad Y = -79.75 + 2.37X$$
$$\text{Station 3} \quad Y = -67.81 + 2.12X$$

where Y = number of eggs and
X = length of fish in millimeters.

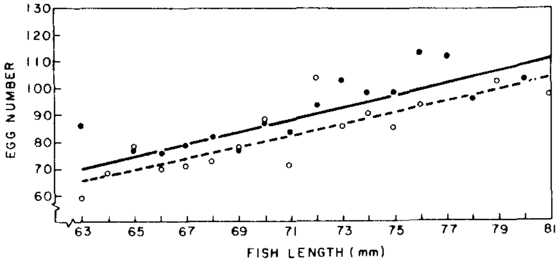

FIGURE 8.—Least squares regression lines indicating the relationship between fish length and number of eggs. Solid line and dots, station 2; dashed line and open circles, station 3.

Coefficient of determination (r^2) values were 0.71 and 0.72 for stations 2 and 3 respectively.

Differences in fecundity relationships between the two stations were implied and analysis of covariance revealed a significant difference (0.01 level) in elevation of the two regressions ($F_{1,28}$ = 19.0). With the presence of atresia, the most obvious theory for this difference would be a slight difference in time of spawning at the two stations. This is suggested by the slightly smaller mean weights of female fish from station 2 sticklebacks at the time of these ovary collections (Table 14). This could be interpreted to mean station 2 females had not matured as much as station 3 fish since female sticklebacks increase their weight by as much as 10% during the maturation period. Atresia would then have acted on the station 2 fish to reduce their fecundity. Any difference in spawning time is probably related to environmental differences between the stations, exemplified by the presence of rooted aquatics at station 3 and their apparent absence at station 2.

Measurements of egg size of six *P. pungitius*, 62-79 mm long, were made on eggs deposited in laboratory aquaria, since Vrat (1949) found stickleback eggs reached maximum size only on extrusion into the water. Eggs were left in the water about 15 min before they were removed and measured under a binocular microscope equipped with an optical micrometer. Egg size appeared to be rather constant with no relationship to size of fish. Egg diameter ranged from 1.53 to 1.98 mm ($\bar{x}$ = 1.76 mm).

Mean weight of ovaries containing ripe eggs was 10.2% and 9.8% of mean fish weight at stations 2 and 3, respectively. Since ovaries in immature fish are very small and some somatic growth had already taken place by spawning time, it is clear that gonad maturation requires a gain in weight of over 10% of the winter weight of the fish. However, early somatic growth in mature females is considerably less than in males (Table 7). It appears that most early annual weight gain in females goes into egg production and rapid somatic growth does not occur until after spawning.

Sex Ratio and Sex Specific Mortality

The sex ratio of sticklebacks was determined for various years of life and for various months because it was obvious from general observation that females predominated in the samples. All 808 fish from which otoliths were extracted were used in the sex ratio calculations. The ratios were:

Age-group	*Male: Female*	*Chi-square*
0	0.930:1	10.54 (7*df*)
I	.809:1	.68 (4*df*)
II	.339:1	22.19 (3*df*)**
III	.125:1	20.57 (3*df*)**
IV	all female	

The χ^2 values for age-groups II and older were significant at the 0.01 level, indicating the ratios were significantly different from 1 to 1.

The sex ratios by month of all fish 1+ and older beginning in April were:

Month	*Male: Female*
April	0.692:1
May	.714:1
June	.366:1
July	.197:1
August	.211:1
November	.137:1
December	.100:1

Monthly length-frequency histograms (Figures 5-6) indicate the presence of two distinct age-groups in most months, the older fish being strung out in an uneven pattern beyond the second mode. However, the second mode disappeared in August as young-of-the-year began to appear in the catches. Since the 2-yr-old fish, which remained after August were predominantly female (Table 16), it appeared the die-off among old fish, as indicated by length-frequency diagrams, was more prevalent among males. The monthly sex ratios of the age-groups comprising most of the spawning population seemed to indicate that such mortality began to occur as early as June with a sharp drop in males in the catchable population through July. However, the die-off did not appear in the length-frequency diagrams until August. This discrepancy might be explained by a differential movement of males onto the spawning grounds in June to set up their territories and/or an increased awareness of the fishing gear by territorial males. Both these explanations could result in decreased male availability to the trawl during the spawning period. However, after the spawning period, males remained low in the catch throughout the rest of the year, indicating a high mortality among males which spawned.

These interpretations are strengthened by two other observations. Males which had spawned previously were identifiable at any time by vestiges of spawning colors on their ventral surface. Few of these individuals were seen in the collections. Also, in a laboratory experiment described by Griswold and Smith (1972), eight males brought off broods to the point where fry were actively swimming about in the aquaria. Seven of these males died within a month of spawning. There was no mortality observed among 10 females which spawned in the laboratory.

TABLE 16.—Ratio of male sticklebacks to females of different age-groups in various months. Annulus formation is complete after July.

Age	Apr.	May	June	July	Aug.	Nov.	Dec.	Mean[1]
0	0.5	1.2	0.7	—	2.0	0.9	0.5	0.9
1	.7	1.1	.2	0.3	.6	.9	1.6	.8
2	.3	.3	0	.1	.2	.4	.4	.3
3	0	0	0	.1	0	.1	.3	.1
4	—	—	0	0	—	—	0	0
Mean[2]	.4	.7	.3	.2	.7	.7	.7	

[1] Weighted for number of fish in each month.
[2] Weighted for number of fish in each age-group.

PARASITE INFECTION

The pleurocercoid stage of the cestode, *Schistocephalus pungitii* Dubinina (Pavlovskii, 1964), is the only parasite generally abundant among ninespine sticklebacks. The procercoid infects numerous species of copepods, and when these are eaten by sticklebacks, the procercoid burrows through the stomach wall to grow as a pleurocercoid in the body cavity. At this stage the parasite is species-specific as, so far as is known, it attacks only the ninespine stickleback. Two months are required for full growth of the pleurocercoid, at which time it may infect a number of fish-eating birds. No other stickleback parasites were noted in the study.

Rate of infection in Apostle Islands sticklebacks was low in 621 fish examined. Only 4 of 362 fish (1.10%) were infected prior to 1 August in all years of the study combined, and 13 of 259 fish (5.01%) were infected after 1 August. Summer and fall infection would intuitively be higher because of greater copepod abundance at that time. The largest pleurocercoid found was 22 mm long and weighed 0.225 g or 14% of the host's weight. Two fish had two pleurocercoids each which made up 18 and 14.5% of the fish's weight, respectively. These parasites were found in 7 male and 10 female sticklebacks. Fish infected at spawning time did not appear to be maturing.

FOOD HABITS OF THE STICKLEBACK AND ASSOCIATED SPECIES

Five papers mention the food of *P. pungitius*. Forbes (1883) found two specimens which contained equal amounts of diptera larvae and cladocerans. Blegvad (1917) found copepods and stickleback eggs predominant in 112 Danish fish. Hynes (1950) reported cladocera, amphipods, and chironomid larvae were the most important food items in fish from an English stream. Bigelow and Schroeder (1953) state that the stickleback feeds voraciously on fish eggs and fry and can be very destructive to other species in fresh water. Anderson and Smith (1971) report crustaceans make up more than 90% of the Lake Superior stickleback diet. In the present study, emphasis was placed on the food habits of sticklebacks and several associated species with which they are most likely to compete or which may be involved in predator-prey relationships with sticklebacks.

In the stomach analyses, contents were removed from the upper esophagus to pyloric sphincter and measured by water displacement in 15-cm³ centrifuge tubes. The contents were then emptied into a gridded petri dish for indentification under a binocular microscope at 10× magnification. Organisms present in small numbers were counted, but larger numbers were estimated from counts in randomly selected squares of the dish. Percentage of each item in the total volume of each stomach was estimated. The data are reported as percentage frequency of occurrence and percentage of total volume for each food item in stomachs containing food.

Invertebrate Abundance

Invertebrates important in the stickleback diet were sampled with the mysis sled concurrently with sticklebacks used in food analysis; therefore, it is assumed that the gear sampled food organisms that were available to sticklebacks. One-mile tows were made with the sled and the invertebrate catch was preserved in 10% Formalin. Invertebrate samples were identified and enumerated on a gridded petri dish in the same manner as stomach contents.

The average number of organisms per 100 m of tow is shown in Table 17 for 18 tows on five dates. The data indicate the extreme abundance of *Pontoporeia affinis* adjacent to the bottom. Although copepods were also abundant, they were usually not as important in mass as either *Pontoporeia* or *Mysis*. Coregonid eggs and fry were found occasionally in fall plankton samples.

Food of the Stickleback

Food analyses of 421 stickleback stomachs in nine different months were made (Table 18).

Fish under 50 mm long fed primarily on *Pontoporeia* and copepods, which made up 79 and 13% of the total food volume, respectively. Cladocerans were of minor importance, and mysids were also present infrequently. Other organisms present in these smaller fish were chironomid and diptera larvae and a filamentous green alga.

Food of sticklebacks 50 mm and over were characterized by a variety of larger food items, suggesting that one factor limiting the diet of young fish is size of food items. *Pontoporeia* taken by the under 50-mm sticklebacks were small in size (4.0 mm average) compared with those found in adult stomachs (6.5 mm).

In these larger fish, *Pontoporeia* made up 61% of the total stomach volume, *Mysis* 21%, copepods 8%, and miscellaneous other items 10%. *Pontoporeia* was the major food item in all months but November. There is a suggestion from late fall and early spring samples that coregonid eggs may be an important food item in the winter. Except for these eggs, there is little to suggest that *P. pungitius* is significantly

TABLE 17.—Average number of invertebrates caught per 100 m in tows along bottom with mysis sled in the Apostle Islands.

[The percentage volume of each item found in stickleback stomachs is in parentheses.]

Organism	29 Apr. 1968	22 July 1968	13 Nov. 1968	29 Apr. 1969	27 June 1969
Number of tows	4	3	4	2	5
Amphipoda:					
Pontoporeia affinis	437,750 (88)	748,260 (61)	117,600 (33)	32,360 (84)	371,660 (69)
Mysidacea:					
Mysis relicta	120 (4)	6,110 (12)	34,280 (60)	1,370 (8)	320 (9)
Cladocera	3,170 (1)	1,040 (4)	280 (0)	30 (2)	2,610 (3)
Bosmina spp.	2,210	910	190	30	2,330
Daphnia spp.	920	120	90	0	90
Others	40	10	0	0	140
Fish eggs	0 (0)	0 (0)	0 (0)	0 (6)	0 (0)
Copepods	43,460 (7)	98,630 (23)	47,210 (0)	23,500 (0)	199,790 (16)
Diptera larvae	0 (0)	0 (0)	0 (6)	0 (0)	0 (3)
Mollusca					
Sphaeriidae	2 (0)	0 (0)	0 (0)	1 (0)	0 (0)
Other	0 (0)	0 (0)	0 (1)	0 (0)	0 (0)

TABLE 18.—Food of Apostle Islands sticklebacks expressed as percentage frequency of occurrence and (in parentheses) percentage of total volume for each food item.

Stickleback length	Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Under 50 mm	Number of Stomachs	0	0	13	18	4	0	5	14	0
	Number empty	0	0	2	1	0	0	0	0	0
	Crustaceans:									
	Pontoporeia affinis			62 (66)	100 (99)	100 (100)			93 (86)	
	Copepoda			15 (11)				100 (97)	7 (3)	
	Cladocera							20 (3)		
	Mysis relicta				6 (1)				7 (7)	
	Insects:									
	Chironomidae			8 (9)					14 (4)	
	Diptera									
	Algae			8 (9)						
50 mm and over	Number of stomachs	31	66	99	27	27	55	20	20	22
	Number empty	11	4	3	3	0	1	1	0	2
	Crustaceans:									
	Pontoporeia affinis	80 (75)	61 (49)	90 (75)	30 (24)	92 (92)	82 (62)	90 (80)	60 (30)	59 (45)
	Hyallela sp			1 (1)						
	Mysis relicta	5 (1)	56 (42)	30 (8)	11 (10)		44 (30)	25 (1)	70 (65)	36 (32)
	Copepoda	5 (2)	12 (3)	8 (13)	52 (38)	4 (2)	5 (1)	5 (12)		
	Cladocera	5 (2)		1 (1)	33 (9)	11 (6)	2 (1)	5 (2)		
	Insects:									
	Chironomidae			9 (1)	11 (5)		16 (3)			
	Other Diptera			2 (1)	7 (6)	4 (1)				
	Ephemeroptera		1 (1)							4 (3)
	Nemotoda						2 (1)			
	Coregonid eggs	5 (2)	12 (3)							27 (20)
	Unidentified	5 (15)	1 (2)	3 (2)	7 (7)		22 (3)	5 (5)	5 (5)	

destructive to fish eggs and fry in Lake Superior as Bigelow and Schroeder (1953) thought was generally the case. Neither eggs nor fry of any other kind were found in stickleback stomachs, although gravid females and young-of-the-year of smelt, trout-perch, slimy sculpins, and pygmy whitefish were taken in the same areas at about the same time as the stickleback stomach samples.

The percentage volume of total stomach contents for each day and for each food item taken in the mysis sled is given in Table 17. *Pontoporeia* was the most important food item except in the November sample. In that month, mysids were the most important food and were more abundant in plankton samples than at any other time. Copepods were most abundant in the June and July samples, and their relative contribution to stickleback diet was also highest in these months. In general, when mysids or copepods became relatively more abundant with respect to themselves or to other zooplankters in the plankton samples, they also become more important in the stickleback diet. This suggests that the stickleback shows no strong food preferences but is adaptable and eats what is most available.

Relation to Food Utilization of Other Forage Species

Juvenile smelt (less than 12.5 cm), trout-perch, and slimy sculpins were found to have diets similar to sticklebacks in Lake Superior (Anderson and Smith, 1971). Since all these species were common in the Apostle Islands, competitive relationships between them and the stickleback could exist. A rank correlation coefficient was used to measure the similarity of food composition between two samples and thus permit examination of interspecific and intraspecific feeding relationships.

Table 19 is an example of the computation as discussed by Snedecor (1956). In the case of

TABLE 19.—An example of the calculation of rank-correlation coefficients.

Food item category	10 stickleback rank	10 trout-perch rank	Difference d	d^2
Pontoporeia	1	1	0	0
Mysis	3	4	−1	1
Copepods	2	3	−1	1
Chironamidae	5	2	+3	9
Cladocera	4	5	−1	1

$n = 5 \qquad \Sigma d = 0 \qquad \Sigma d^2 = 12$

$$r_s = 1 - \frac{6(12)}{5(25-1)} = 1 - \frac{72}{120} = 0.40$$

a tie in importance of any two categories, the larger item was ranked first. An r_s value of +1.0 indicates that the various food categories were eaten in the same order of preference, and as r_s approaches −1.0, there is no agreement in order of occurrence.

To test the hypothesis that fish of the same species eat the same things in different areas, 10 randomly selected fish caught from one station within 3 days were compared. In interspecific tests, 10 fish of each species taken at the same station on the same day were used. Except for smelt, only adults were used in the tests because juveniles of other species were not completely available to the gear and not taken in large enough quantities to test.

Analyses of individual tests were not made; instead the results from several comparisons (N in Table 20) were combined and a test made using the combination of probabilities discussed by Snedecor (1956:216). The sum of the natural logarithms of the probabilities associated with each of several comparisons is multiplied by −2, and the resulting values have a chi-square distribution with two degrees of freedom for each comparison. Pearson (1924) presents a figure which allows graphical calculation of probabilities associated with r_s.

Intraspecific correlations were significant for all comparisons (Table 20). Indications are that food habits among individuals of the same species were almost identical within the Apostle Islands.

Significant interspecific correlations were found between sticklebacks and slimy sculpins in spring and summer and sticklebacks and

TABLE 20.—Food composition similarity measured by rank-correlation coefficients (r_S) between sticklebacks and other Apostle Islands species. (N equals the number of individual tests for each comparison, and n equals the number of food categories in each comparison.)

Comparison	N	n	Mean r_S	Chi-square
1. Between adult sticklebacks of stations 2 and 3	5	6	+0.94	36.89**
2. Between adult trout-perch from two stations	3	5	+.83	16.81*
3. Between juvenile smelt from two stations	3	4	+.85	16.98*
4. Between adult sculpins from two stations	5	6	+1.00	—
5. Between adult sticklebacks and other species within each catch:				
Spring:				
Trout-perch	7	5	+.70	30.89*
Smelt	10	4	+.40	34.29
Sculpins	10	6	+.89	62.02**
Summer:				
Trout-perch	4	5	+.43	13.94
Smelt	2	4	−.30	6.54
Sculpins	10	6	+.89	62.02**
Fall:				
Trout-perch	4	5	+.33	13.28
Smelt	4	4	+.40	13.72
Sculpins	5	6	+.37	16.87

* Significant at the 0.01 level.
** Significant at the 0.005 level.

trout-perch in spring. The significant rank correlation does not necessarily indicate the amount of competition for food, but merely the potential for such competition. For competition to occur, there must be a demand by more than one organism for the same food in excess of immediate supply. It can only be said that since the abundance of sticklebacks and slimy sculpins are positively correlated in the index catches and their food relationships are similar, the possibility of competition between the two species exists during some seasons. The actual existence of competition is highly questionable because of the apparent abundance of *Pontoporeia*, the number one food item, and the apparent adaptability of the stickleback in food utilization. The drop in correlation in the fall was due to greater use of chironomids by sculpins.

While the correlation with trout-perch also indicates potential competition for food, their abundance in the index trawl samples was negatively correlated and Dryer (1966) found trout-perch and sticklebacks to have different bathymetric distributions. While the trout-perch and sticklebacks utilized the same foods in spring, their secondary foods were different in summer and fall. Anderson and Smith (1971) found trout-perch fed on wider variety of food items than sticklebacks in the Apostle Islands. This combined evidence seems to indicate that competition between these two species is also unlikely.

Sticklebacks as Forage for Other Fish

Several fish species which occur in Lake Superior have been reported to feed on sticklebacks at various locations. These include lake trout; brown trout, *Salmo trutta* L.; rainbow trout, *Salmo gairdneri* Richardson; burbot, *Lota lota* (L.); and various sculpins. Of these, the lake trout was the only species which fed heavily on sticklebacks in the Apostle Islands.

Dryer, Erkkila, and Tetzloff (1965) related a change in diet in juvenile Lake Superior lake trout to their size. The diet, primarily a crustacean-insectivorous type in small trout, became piscivorous in larger fish.

In the present study, sticklebacks were found in 7.5% (33) of 436 lake trout less than 28 cm (11 in.) long (TL). Only 3.5% of the volume of stomachs from 142 fish under 25.4 cm (10 in.) was sticklebacks. In 294 trout from 25.4 to 28.0 cm, sticklebacks made up 32% of the volume of the diet.

Sticklebacks were a major part of the diet of lake trout from 28.0 to 38.0 cm (11.0 to 14.9 in.) (Figure 9). *P. pungitius* made up 39% of volume in the diet and were found in 42% of the 176 trout which contained food. Smelt was the second most abundant fish species in the diet of 28- to 38-cm trout. The food habits of trout remained about the same for all ice-free months (Anderson and Smith, 1971).

The major food of trout longer than 38 cm was smelt. Of 30 trout in this size range, 69% of the stomach contents were smelt remains. Sticklebacks were found in five of these fish and made up 17% of the volume. Nineteen adult sticklebacks and two sculpins were found in one 50-cm (19.7 in.) trout. Sticklebacks eaten by trout were all age-group I or older. No stickleback eggs or age-group 0 fish were found in over 4,500 trout stomachs sampled on the Lake Superior project.

The explanation of the absence of small sticklebacks in the trout diet is probably one of dis-

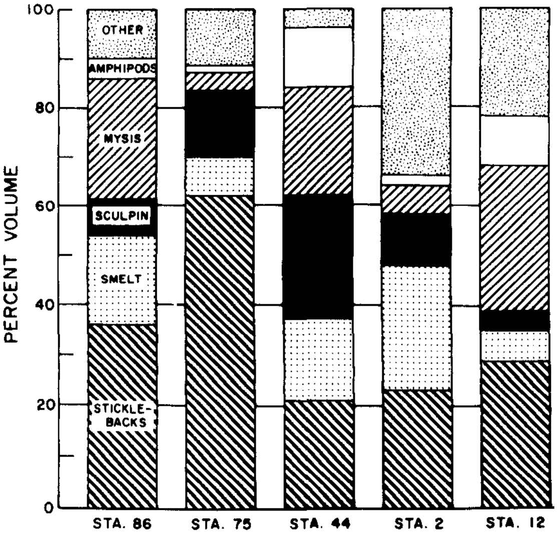

FIGURE 9.—Percent volume of various food items found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual BCF index trawling cruises.

tribution. After hatching, the young sticklebacks congregate in the shallow sandy areas where they are unavailable to lake trout and most other species. By the time they leave the shallow water in late fall, they have grown to 45 mm or more. It is at this length that they begin to appear in trout stomachs the following spring.

Smaller trout cannot feed well on sticklebacks once the latter become available after a summer's growth, because of the protective spines. This inability explains the relative unimportance of sticklebacks in the diet of small trout. Similarly, Hoogland, Morris, and Tinbergen (1957) found young northern pike, *Esox lucius* L., rejected sticklebacks, first exhibiting a negative reaction to mechanical stimuli upon contact with the spines and then a visual avoidance. Upon reaching a certain size, the pike preferentially take sticklebacks (Frost, 1954). A discussion by Fortunatova (1959) supports this theory. The dietary shift to smelt by larger trout can be explained by assuming the optimum size of the prey increases as the trout grow larger.

Compared to all lake trout over 28 cm long taken from a number of trout index stations, fish from stations 75 and 86 ate a high percentage of sticklebacks (Table 21, Figure 9). At station 86, considered the best trout nursery area in the Apostle Islands, sticklebacks were the predominant food item even though juvenile smelt were more abundant in the index trawl samples (Table 9). At station 75, the second most important nursery area, sticklebacks were very abundant, and they made up more than 60% of the trout diet. Station 12 sticklebacks and smelt were about equal in the index catch, but sticklebacks were much more important in the trout diet. At station 44, the predominant forage fish in the trawl samples was sculpins, and these were dominant in trout stomachs. At this station, sticklebacks were comparatively rare in occurrence, but still made up 21% of the volume of the trout diet. It might be assumed from station 44 data that sculpins are an important item in the diet and that trout will substitute sculpins when sticklebacks and smelt are not readily available. However, the stations with high sculpin abundance relative to stickleback abundance do not support large numbers of trout. From these data, it appears that the availability of sticklebacks at the various stations is probably important in the selection of these areas by lake trout as

TABLE 21.—Percent frequency of occurrence and (in parentheses) percent total volume for each food item found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual Bureau of Commercial Fisheries index trawling cruises.

Item	Station 86	Station 75	Station 44	Station 2	Station 12
Number of stomachs	77	45	24	51	33
Number empty	20	3	0	0	0
Crustaceans:					
Mysidacea	35 (25)	15 (4)	33 (22)	16 (6)	64 (29)
Amphipoda	18 (4)	8 (<1)	17 (12)	2 (<1)	36 (10)
Copepoda	—	1 (<1)	—	—	3 (<1)
Fish:					
Smelt	14 (18)	9 (8)	12 (16)	21 (25)	6 (6)
Stickleback	30 (36)	64 (62)	17 (21)	21 (23)	33 (29)
Sculpin	6 (7)	13 (13)	21 (25)	12 (10)	6 (4)
Unidentified	9 (8)	15 (11)	17 (3)	27 (36)	24 (19)
Fish eggs	—	—	—	1 (<1)	—
Insects:					
Chironomidae	6 (<1)	6 (<1)	2(<1)	—	3 (<1)
Coleoptera	1 (<1)	—	—	—	—
Trichoptera	1 (<1)	1 (<1)	—	—	—
Other	1 (<1)	7 (<1)	—	1 (<1)	6 (3)
Miscellaneous		1 (<1)	—	—	—

nursery areas, although other factors are also important because there are many areas where sticklebacks are abundant and trout are not. Conversely, no good trout nursery area are known where sticklebacks are not abundant.

The importance of the stickleback as a food item for the lake trout in the Apostle Islands appears to be substantial while the latter are between 28 and 38 cm long. No information is available, however, to indicate the amount of substitution which would occur if the sticklebacks were less available.

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