c.2

Age, Growth, and Food of Threespine Sticklebacks *(Gasterosteus aculeatus)* in Three Lakes of Central Newfoundland, Canada

Dept. of Fisheries & Oceans
Regional Library
NFLD.

P. M. Ryan

Fisheries Research Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, Newfoundland A1C 5X1

October 1984

Canadian Technical Report of Fisheries and Aquatic Sciences No. 1325

Fisheries and Oceans Pêches et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of the Department of Fisheries and Oceans, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in *Aquatic Sciences and Fisheries Abstracts* and indexed in the Department's annual index to scientific and technical publications.

Numbers 1–456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457–714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715–924 were issued as Department of Fisheries and the Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page. Out-of-stock reports will be supplied for a fee by commercial agents.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques du ministère des Pêches et des Océans, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications complètes. Le titre exact paraît au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la revue *Résumés des sciences aquatiques et halieutiques*, et ils sont classés dans l'index annual des publications scientifiques et techniques du Ministère.

Les numéros 1 à 456 de cette série ont été publiés à titre de rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre. Les rapports épuisés seront fournis contre rétribution par des agents commerciaux.

Cat. #72226

Canadian Technical Report of

Fisheries and Aquatic Sciences 1325

Dept of Fisheries & Oceans
JAN 25 1985
Regional Library, Nfld

October 1984

AGE, GROWTH, AND FOOD OF THREESPINE STICKLEBACKS (Gasterosteus aculeatus) IN THREE LAKES OF CENTRAL NEWFOUNDLAND, CANADA

by

P. M. Ryan

Fisheries Research Branch

Department of Fisheries and Oceans

P.O. Box 5667

St. John's, Newfoundland A1C 5X1

This is the eighty-fourth Technical Report from

Fisheries Research Branch, St. John's, Newfoundland.

(c)Minister of Supply and Services Canada 1984

Cat. No. Fs 97-6/1325 ISSN 0706-6457

Correct citation for this publication:

Ryan, P. M. 1984. Age, growth, and food of threespine sticklebacks (*Gasterosteus aculeatus*) in three lakes of central Newfoundland, Canada. *Can. Tech. Rep. Fish. Aquat. Sci.* 1325: iv + 16 p.

CONTENTS

ABSTRACT

Ryan, P. M. 1984. Age, growth, and food of threespine sticklebacks (Gasterosteus aculeatus) in three lakes of central Newfoundland, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1325: iv + 16 p.

The age structure, life span, growth, and food of threespine sticklebacks in three small lakes in central Newfoundland were studied. Fish could be aged from length-frequency distributions but otoliths were not satisfactory for that purpose. The first hatching date was late May to early June. Fish spawned in their second or third year and had a maximum life span of about two and one-half years. Little variation in growth occurred between years or among lakes and growth rates were near the middle of the range experienced by populations of this species. Most individuals fed on benthic or pelagic cladocerans and chironomid larvae.

RÉSUMÉ

Ryan, P. M. 1984. Age, growth, and food of threespine sticklebacks (Gasterosteus aculeatus) in three lakes of central Newfoundland, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1325: iv + 16 p.

Cet article porte sur la composition de l'âge, la durée de vie, la croissance et l'alimentation de l'épinoche à trois épines peuplant trois petits lacs du centre de Terre-Neuve. Il a été possible de déterminer l'âge des poissons d'après la distribution de fréquence des longueurs, mais les otolithes n'ont pu servir à cette fin. La première éclosion s'est produite entre la fin de mai et le début de juin. Les épinoches frayent au cours de leur deuxième ou troisième année et vivent deux ans et demi au maximum. La croissance a peu varié d'une année à l'autre et d'un lac à l'autre. Les taux de croissance se situaient près de la moyenne pour les populations de cette espèce. La plupart des individus se nourrissaient de cladocères benthiques et pélagiques et de larve de chironomidés.

INTRODUCTION

Little information exists on the ecology of threespine sticklebacks in Newfoundland even though they are, after brook trout (Salvelinus fontinalis), the most widely distributed fish in Newfoundland's fresh waters (Scott and Crossman 1964). Potential relationships of threespine sticklebacks to economically valuable salmonids include those of predator (Laurent 1972), prey (Ryan 1980), competitor (Maitland 1965; Coad and Power 1973a), and parasite co-host (Cone and Ryan 1984). The literature on threespine sticklebacks has been reviewed extensively by Wootton (1976). However, detailed information on the ecology of this species in the fresh waters of eastern Canada appears to have been limited to Quebec (Coad and Power 1973a, b).

Reports on populations of threespine sticklebacks in Newfoundland have included records of meristic and morphometric characteristics (Penczak 1962; Van Vliet 1970; Garside and Hamor 1973), parasitic fauna (Threlfall 1968; Hanek and Threlfall 1970; Cone and Ryan 1984) and the lengths and weights of individuals (Pepper 1976). Pepper (1976), as part of a study of the habitat of Atlantic salmon (Salmo salar), presented length-frequency distributions of threespine sticklebacks which suggested the presence of three age groups (0, 1, 2) in a pond and stream in the watershed of the Gander River. However, he was not able to verify the ages of these fish and cautioned that comparisons of his data to other lakes or years might not be valid because of the short period of study. Pepper suggested that poor salmon fry survival in ponds may be caused by competition for food between salmon and sticklebacks although comparisons of diet were not made. Thus, there is a need for ecological information on the threespine stickleback in Newfoundland. This report documents the age composition, life span, growth, and food of threespine sticklebacks in three lakes at the headwaters of the Northwest Gander River, Newfoundland. It is the first such study of this species in Newfoundland.

THE STUDY AREA

The Experimental Ponds Area includes three small lakes and their tributary streams at the headwaters of the Northwest Gander River, some 155 km from its outlet to the Atlantic Ocean on the northeast coast of Newfoundland (Fig. 1). Limnological studies in the Area have been conducted since 1977 (Ryan 1982; Cone and Ryan 1984; Ryan 1984; Ryan and Wakeham 1984). The study lakes (Table 1) are shallow, oligotrophic, postglacial waters usually ice covered from December to April. Their water quality is typical of Newfoundland's many brown-water lakes (Jamieson 1974). Predominant macrophytes are the yellow water lily (Nuphar variegatum), the pipewort (Eriocaulon septangulare), the pondweed (Potamogeton oakesianus), and the bureed (Sparganium spp.). In addition to threespine sticklebacks, fish species present are the brook trout (Salvelinus fontinalis), the Atlantic salmon (Salmo salar), and the American eel (Anguilla rostrata).

MATERIALS AND METHODS

Sticklebacks were captured with a 4.8 mm square mesh seine net, near the end of August at each of three locations in Spruce and Headwater ponds from

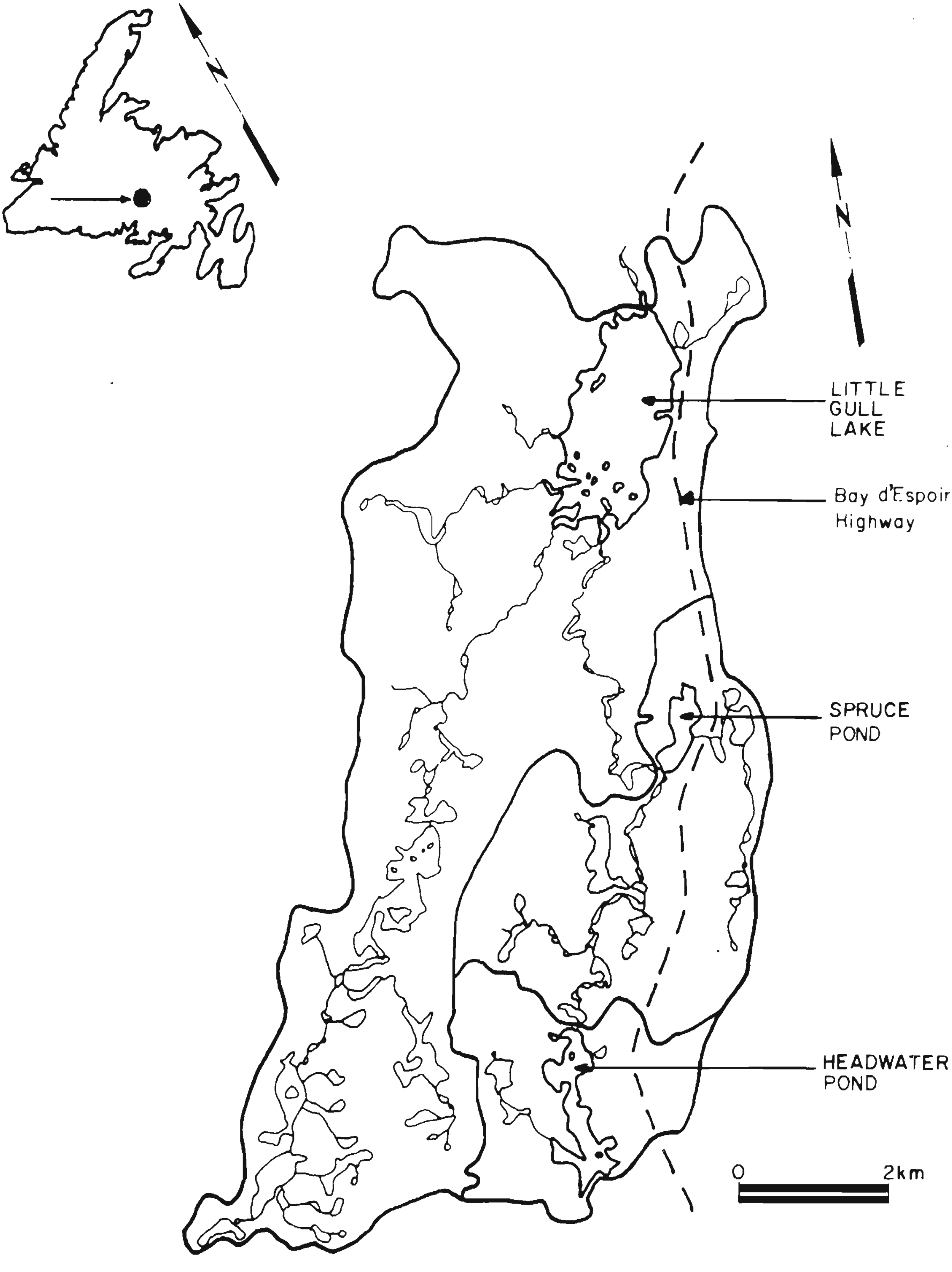

Fig. 1. Watershed of the Experimental Ponds Area, central Newfoundland. The catchment basin of each study lake is outlined.

Table 1. Selected physical and chemical descriptors of the study lakes. Values for chemical descriptors are the means of all values (number = N) encountered May-October, 1977-81. Based on Ryan and Wakeham (1984).

	Headwater Pond (N=66)	Spruce Pond (N=105)	Little Gull Lake (N=7)
Latitude	48°16'	49°19'	48°21'
Longitude	55°29'	55°28'	55°29'
Water area (ha)	76.1	36.5	306.5
Volume ($m^3 \times 10^{-3}$)	872	364	5328
Maximum depth (m)	3.3	2.1	6.3
Mean depth (m)	1.1	1.0	1.7
pH	6.4	6.3	6.2
Conductance ($\mu S\ cm^{-1}$)	33	33	62
Alkalinity (ppm)	4.3	4.2	2.7
Calcium (ppm)	3.3	2.1	1.9

1978 to 1981 and in Little Gull Lake in 1978 and 1979. Additional collections were made throughout the summer of 1979 in Spruce and Headwater ponds with a seine net constructed of fibreglass fly-mesh used for window screening . Fish were preserved in 70% alcohol for a minimum period of three weeks. Total lengths (mm) of all fish were obtained and modes in the length-frequency distributions were used to assign ages to the fish (Tesch 1971). A sagittal otolith was removed from each individual in a subsample of approximately ten fish from each cm length interval. Otoliths were mounted on plasticine and examined dry or in glycerine, alcohol, or water. Ages were assigned using the criteria of Jones and Hynes (1950). Individuals in the late summer subsamples were weighed to the nearest mg and weight-length regressions were compared by analysis of covariance (Dixon and Massey 1969). A further subsample of approximately 10 fish, spanning the range of fish lengths, was selected from the late summer collection from each lake, each year and stomach contents were examined.

RESULTS AND DISCUSSION

AGING AND LIFE HISTORY

Length-frequency distributions of fish taken throughout the summer of 1979 (Fig. 2) were composed of nearly discrete modes shifting position as growth occurred, thus permitting an accurate assessment of the ages of most fish. The distributions indicated a first hatching date of late May to early June and a maximum life span of about two and one-half years. In early June, the distributions had two distinct modes. A third mode, young-of-the-year fish, appeared in the catches in late June. The near disappearance of individuals in the largest mode as the summer progressed suggested that the majority of fish spawned at the beginning of their second or third summer with few surviving the third summer.

Newly hatched larvae vary in length from 3 to 5 mm and attain lengths of about 11 mm in 23 days at 18° to 19°C (Wootton 1976). The smallest individuals captured in early August were indicative of the usual extended spawning period of this species. Sticklebacks usually do not reach maturity until they are about 40 mm (Craig-Bennett 1931; Baggerman 1957). Thus, those that grew slowly would not be capable of spawning until their third summer. In the Experimental Ponds Area, the smallest fish observed with eggs was 36 mm at the end of August.

This life-history pattern is similar to that of other eastern Canadian freshwater populations. Pepper (1976) first encountered underyearlings in seine net samples on July 9 in a lake of the Gander River system downstream from the study area. Length-frequency distributions in those samples were suggestive of only three year-classes. Coad and Power (1973a) described a maximum life span of "two years and some months" for several populations in the Matamek watershed of Quebec. They reported that spawning occurred in July of the third year of life. Variation in age at first spawning is common, varying with local conditions and growth rate (Wootton 1976).

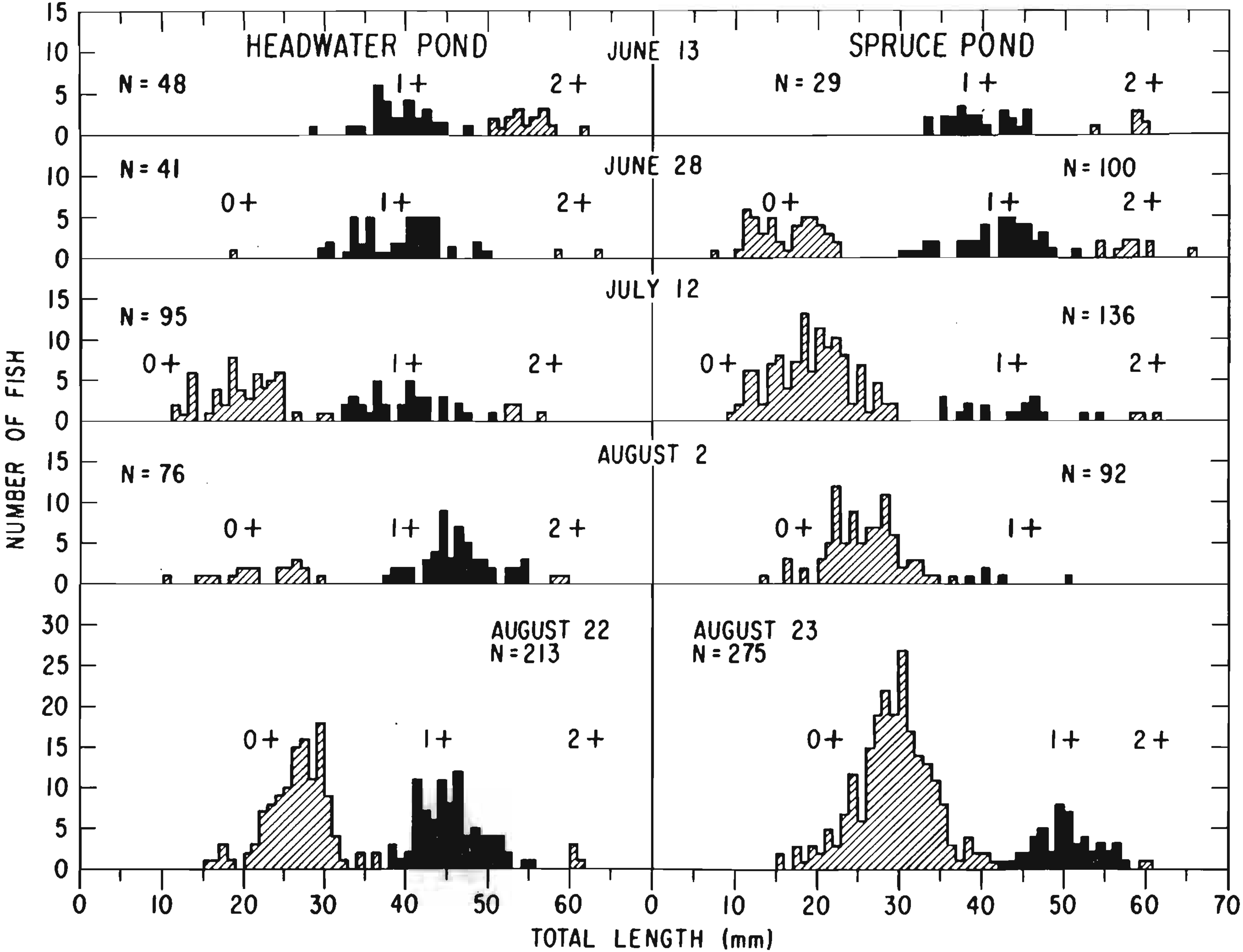

Fig. 2. Length-frequency distributions of threespine sticklebacks seine netted throughout the summer of 1979 in Headwater and Spruce ponds. Ages assigned to the fish are indicated.

The assignment of ages to the fish using otoliths resulted in an unacceptably high and variable error rate. For example, fish from the smallest mode in the length-frequency distribution from Spruce Pond on June 28, 1979 (Fig. 2) were obviously underyearlings. However, of eleven of these fish aged from otoliths, eight were assigned to age-group 0, two to age-group 1, and one to age-group 2; an error rate of 27%. Six fish in the second larger mode were assigned to age-groups 1 (one fish), 2 (four fish), and 4 (one fish). Three fish of 55 to 65 mm were assigned to age-groups 2 and 4. Both otoliths from a 22 mm fish from Spruce Pond on August 2 exhibited an opaque centre, four transparent bands, and three opaque bands. Similarly, obvious underyearlings less than 34 mm from Headwater Pond on August 22 were assigned to age-groups 1 (13 fish) or 2 (three fish).

Such variation between obviously correct ages shown by the length-frequency distributions and those indicated by otoliths may have been due to a variety of external and internal factors associated with the formation of growth checks on bony tissues (Tesch 1971). Pepper (1976) found threespine stickleback otoliths too minute and brittle to permit accurate annulus counting. Munzing (1959) reported that otoliths from some migratory populations were unsuitable for aging. Jones and Hynes (1950) found length-frequency distributions unsuitable for age determination in a population in northwest England because of large overlap in the lengths of age groups. Otoliths were considered "satisfactory" for this purpose, although "false" or misleading rings were often present on the otoliths. Other investigators have described populations in which both length-frequencies and otoliths were suitable for aging (Greenbank and Nelson 1959; Coad and Power 1973a; Allen and Wootton 1982). In the present study, ages indicated by otoliths were considered unsuitable. Subsequently, ages were assigned on the basis of the length-frequency distributions.

COMPARATIVE GROWTH

Length-frequency distributions of fish collected in the late summer from Headwater and Spruce ponds (Fig. 3) and Little Gull Lake (Fig. 4) exhibited, for the most part, modes of minimal overlap indicative of age structure; consistent with modes in the samples taken throughout the summer of 1979. Accordingly, ages were assigned on the basis of length as follows: Headwater Pond 0+ = < 37 mm, 1+ = 37-57 mm, 2+ = > 57 mm; Spruce Pond 0+ = < 42 mm, 1+ = 42-58 mm, 2+ = > 58 mm; Little Gull Lake 0+ = < 47 mm, 1+ = 47-63 mm, 2+ = > 63 mm. Some fast or slow-growing fish may have been incorrectly aged but aging errors, if they occurred, were considered to be negligible. Positive bias in the mean length of age-group 0 such as that in Little Gull Lake in 1978 (Fig. 4) was likely a result of the smaller fish escaping through the seine-net mesh during some collections. Most samples of young-of-the-year exhibited little or no obvious skew.

Little variation in growth in length was evident within a given lake from year to year or from lake to lake but lengths attained by the first two age groups were greatest in Little Gull Lake and least in Headwater Pond (Table 2). Few fish in their third year were captured. Lengths attained by threespine sticklebacks of various ages in the Experimental Ponds Area were

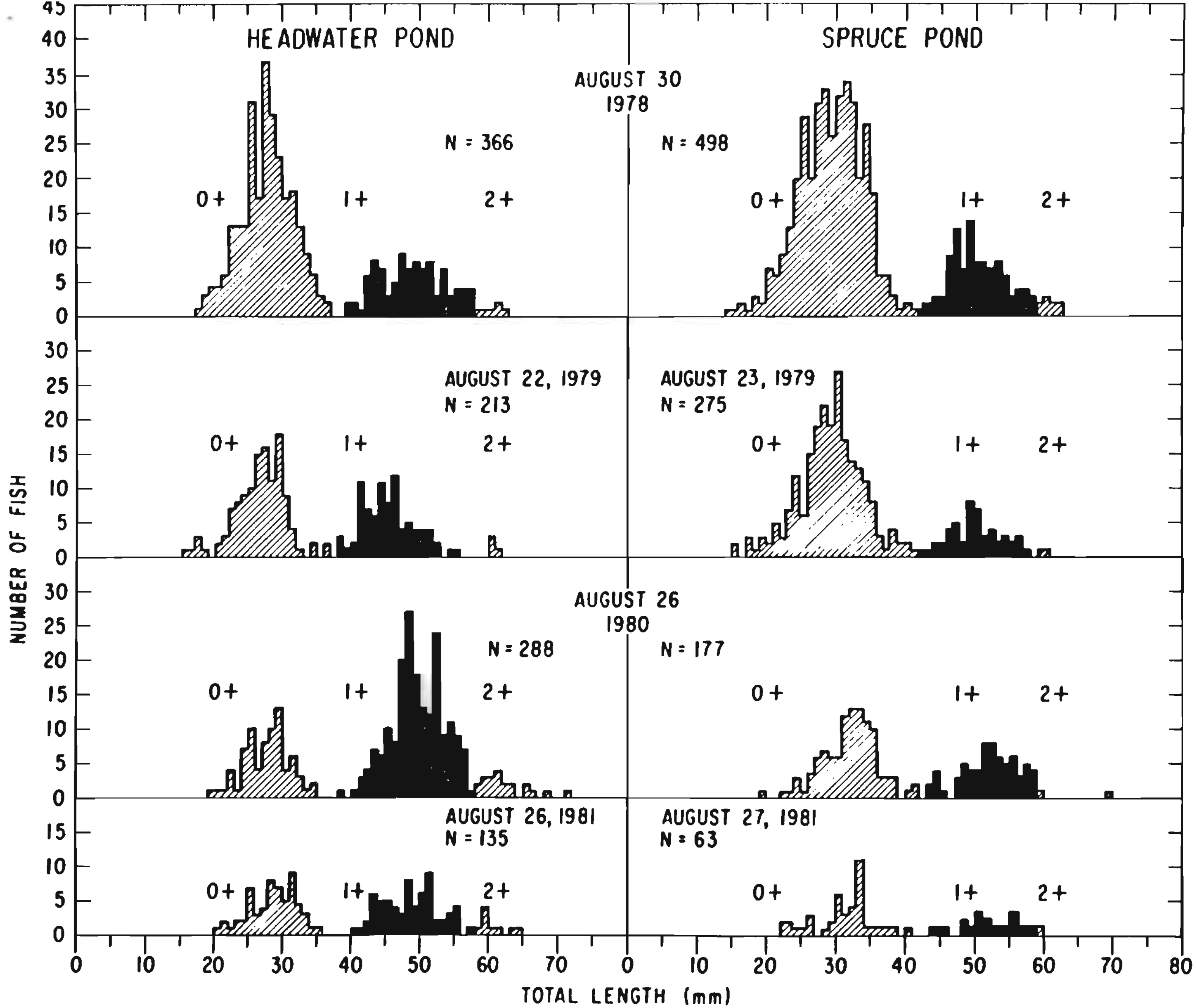

Fig. 3. Length-frequency distributions of annual collections of threespine sticklebacks from Headwater and Spruce ponds. Ages assigned to the fish are indicated.

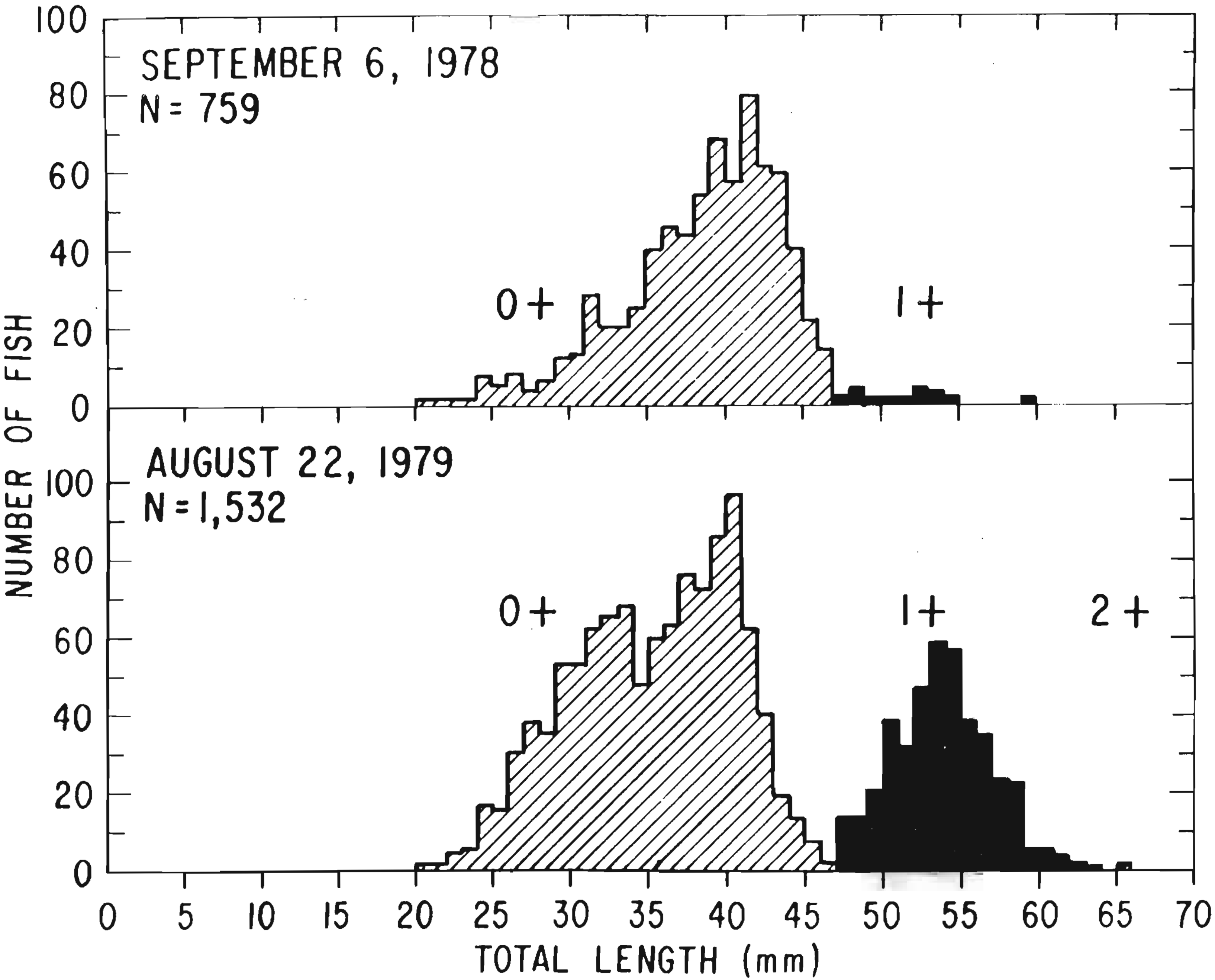

Fig. 4. Length-frequency distributions of threespine sticklebacks from Little Gull Lake. Ages assigned to the fish are indicated.

Table 2. Lengths (mm) of the age groups of threespine sticklebacks from the study lakes August-September, 1978-81 as determined from the length-frequency distributions of seine-netted fish. SN and N indicate the standard deviations about the means and the number of fish examined, respectively.

Year of capture		Headwater Pond 0	Headwater Pond 1	Headwater Pond 2	Spruce Pond 0	Spruce Pond 1	Spruce Pond 2	Little Gull Lake 0	Little Gull Lake 1	Little Gull Lake 2
1978	$\bar{x}$	27.1	48.4	60.2	28.8	50.0	60.4	38.1	51.1	
	SN	3.7	4.7	1.5	4.6	3.8	1.1	4.9	3.1	
	N	262	98	6	386	103	9	740	19	
1979	$\bar{x}$	27.1	45.8	61.3	28.8	49.7	60.7	34.7	53.3	65.0
	SN	3.6	3.9	0.5	4.7	3.6	2.1	5.2	3.2	0.0
	N	121	88	4	222	50	3	1107	423	2
1980	$\bar{x}$	27.2	49.2	62.0	31.5	51.6	64.0			
	SN	3.2	3.8	3.4	4.0	4.0	7.1			
	N	76	191	21	107	68	2			
1981	$\bar{x}$	28.2	48.2	60.2	30.6	51.2	59.0			
	SN	3.4	4.0	2.1	4.2	4.3	0.0			
	N	60	66	9	42	20	1			
1978-81	$\bar{x}$	27.3	48.2	61.3	29.3	50.5	60.9	36.1	53.2	65.0
	SN	3.6	4.2	2.8	4.6	3.9	2.6	5.4	3.2	0.0
	N	519	443	40	757	241	15	1847	442	2

near the middle of the wide range reported for freshwater populations of this species elsewhere (Fig. 5).

The dependence of stickleback growth on environmental and genetic influences is not completely understood (Wootton 1976). It seems probable that the small differences in growth rates among the Experimental Ponds Area stocks are primarily due to differences in environments since the stocks are not widely separated.

A small amount of variation in weight with respect to length occurred within and among lakes (Table 3). Intercepts or slopes changed slightly within each lake, possibly as a result of environmental changes. With the data of all years combined, there was no difference in weight of fish of a given length between Headwater and Spruce ponds. In contrast, fish of the same length from Little Gull Lake tended to be heavier.

These small between-lake differences in growth may account for the much lesser abundance of 2+ fish in the Little Gull Lake samples. In many populations, a more rapid growth and resultant earlier sexual maturation results in a shorter life span since all or most adults die after spawning (Wootton 1976; Allen and Wootton 1982).

FOOD

Sticklebacks in the Experimental Ponds Area fed on a wide range of food items (Table 4) as in lakes and streams elsewhere (Wootton 1976). The majority in Headwater and Spruce ponds had been feeding on benthic microorganisms at the time of capture. Pelagic food was taken by fewer fish. Most fish had been feeding on benthic cladocerans and chironomid larvae. In contrast, most of the Little Gull Lake sticklebacks had been feeding on pelagic daphnids and bosminids and fewer had fed on benthic chironomid larvae. Differences in fish diet among these lakes may be a function of food availability. Threespine sticklebacks are facultative omnivores (Scott and Crossman 1973; Wootton 1976) and daphnids were more abundant in Little Gull Lake zooplankton samples taken in 1978 and 79 than they were in Headwater and Spruce ponds (Ryan 1982).

The differences in diet among these stocks suggest an explanation for the more rapid growth in length and weight of fish from Little Gull Lake. The absence of copepods and gastropods in the sticklebacks from Little Gull Lake indicates that these fish would have been less susceptible to parasite infection and thus potentially faster growing than their counterparts in Headwater and Spruce ponds. These food items are intermediate hosts of parasites (Hoffman 1967) which may reduce the growth rate of their host (Pennycuick 1971). Parasites which have a potential for growth inhibition have been identified in sticklebacks from Headwater Pond (Cone and Ryan 1984).

Threespine sticklebacks in the study lakes share a small part of the food resource with salmonids. In Headwater and Spruce ponds, 62-83% of salmon and trout of 5-37 cm fed on Odonata nymphs while none contained plankton and only 1-6% had eaten Diptera larvae (Ryan unpublished). Other food items were shared to a small extent. Of the brook trout in both lakes, 27-32% had fed on gastropods but only 7% of the salmon parr from Spruce Pond contained snails.

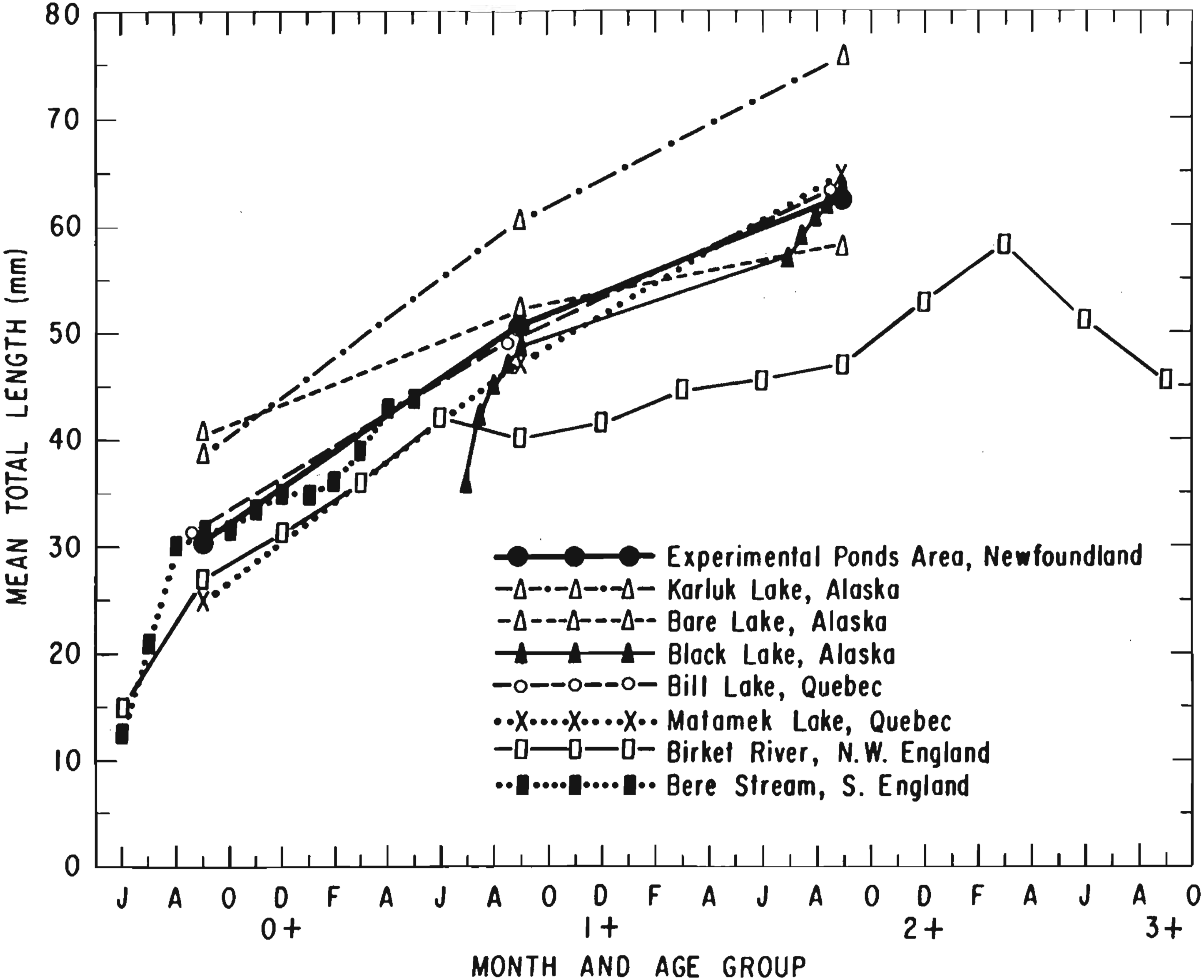

Fig. 5. Comparative growth in length of freshwater populations of threespine sticklebacks in the Experimental Ponds Area (present study), Karluk and Bare lakes, Alaska (Greenbank and Nelson 1959), Black Lake, Alaska (Narver 1966), Bill and Matamek lakes, Quebec (Coad and Power 1973a), Birket River, England (Jones and Hynes 1950), and Bere Stream, England (Mann 1971).

Table 3. Regressions of $\log_{10}$ weight (g) on $\log_{10}$ length (mm) of threespine sticklebacks seined in the study lakes, August-September, 1978-81. Within a given row, slopes or intercepts with dissimilar superscripts are significantly ($p < 0.05$) different from one another.

	Headwater Pond				Spruce Pond				Little Gull Lake			
Year of capture	Slope	Intercept	No. of fish	r^2	Slope	Intercept	No. of fish	r^2	Slope	Intercept	No. of fish	r^2
1978	3.54	-6.13	53	0.96	3.47	-6.02	61	0.97	3.07^{a}	-5.37^{a}	56	0.97
1979	3.38	-5.76	44	0.97	3.44	-5.94^{a}	51	0.98	3.30	-5.68^{b}	43	0.98
1980	3.66	-6.43	44	0.95	3.32	-5.85	39	0.93				
1981	3.41	-5.91	56	0.98	3.61	-6.23	60	0.97				
1978-81	3.46	-6.00	197	0.94	3.46	-6.01	211	0.96	3.23^{a}	-5.59^{a}	99	0.97
Between year comparisons within lakes	Equal $p = 0.1697$	Not equal $p = 0.0001$			Equal $p = 0.2753$	Not equal $p = 0.0001$			Equal $p = 0.0418$	Not equal $p = 0.0036$		

Table 4. Stomach content analysis of threespine sticklebacks seined in the study lakes, August-September, 1978-81. Figures indicate the number of stomachs containing a given food item expressed as a percentage of the number of stomachs containing food items.

Food item	Headwater Pond 1978-81	Spruce Pond 1978-81	Little Gull Lake 1978-79	Three lakes 1978-81
Chydoridae	65.8	59.0	23.8	54.1
Chironomidae larvae	42.1	43.6	28.6	33.7
Cladocera remains	36.8	33.3	9.5	29.6
Amphipoda	28.9	33.3	19.0	28.6
Insecta remains	26.3	30.8	9.5	24.5
Cyclopoida	28.9	28.2	-	22.4
Pelecypoda	23.7	17.9	9.5	18.4
Gastropoda	28.9	15.4	-	17.3
Daphnidae	10.5	5.1	47.6	16.3
Macrothricidae	21.1	17.9	4.8	16.3
Diptera pupae	7.9	30.8	4.8	16.3
Sididae	21.1	5.1	4.8	10.2
Bosminidae	2.6	7.7	28.6	10.2
Ephemeroptera nymphs	5.3	15.4	9.5	10.2
Trichoptera larvae	10.5	7.7	-	7.1
Harpacticoida	10.5	5.1	-	6.1
Ostracoda	13.2	2.6	-	6.1
Arachnoidea	5.3	7.7	-	5.1
Anisoptera nymphs	5.3	2.6	-	3.1
Holopedidae	-	-	4.8	1.0
Calanoida	2.6	-	-	1.0
Bacillariophyta	-	-	4.8	1.0
Rotifera	-	2.6	-	1.0
Seeds	2.6	-	-	1.0
No. stomachs examined	40	41	21	102
No. empty stomachs	2	2	-	4

These data suggest that little dietary overlap exists between salmonids and threespine sticklebacks under natural conditions in small Newfoundland lakes. However, in lakes stocked with underyearling Atlantic salmon by man, food competition may be of concern since these salmon, normally absent from lakes, may feed heavily on crustacean zooplankton (Arnemo et al. 1980; Pepper pers. comm.) as do Pacific salmon (English 1983). Accordingly, population densities and food of Newfoundland's second most common freshwater fish, the threespine stickleback, should be examined prior to and after the introduction of Atlantic salmon fry to selected lakes.

ACKNOWLEDGMENTS

M. Barnes, B. Bennett, L. Cole, B. Meaney, D. Riche, and D. Wakeman provided technical assistance with data collection and processing. G. Marshall and G. Somerton assisted with statistical analyses. K. Harding typed the report. G. King, H. Mullett, and D. Wakeham prepared the figures. E. T. Garside, R. J. Gibson, M. F. O'Connell, T. R. Porter, and three anonymous individuals reviewed the manuscript.

REFERENCES

Allen, J.R.M., and R. J. Wootton. 1982. Age, growth and rate of food consumption in an upland population of the three-spined stickleback, Gasterosteus aculeatus L. J. Fish. Biol. 21: 95-105.

Arnemo, R., C. Puke, and N. G. Steffner. 1980. Feeding during the first weeks of young salmon in a pond. Arch. Hydrobiol. 89(1-2): 265-273.

Baggerman, B. 1957. An experimental study on the timing of breeding and migration in the threespined stickleback (Gasterosteus aculeatus L.). Arch. neerl. Zool. 12: 105-318.

Coad, B. W., and G. Power. 1973a. Observations on the ecology of lacustrine populations of the threespine stickleback (Gasterosteus aculeatus L., 1758) in the Matamek River System, Quebec. Nat. can. 100: 437-445.

1973b. Observations on the ecology and phenotypic variation of the threespine stickleback, Gasterosteus aculeatus L., 1758, and the blackspotted stickleback, G. wheatlandi Putnam, 1867, (Osteichthyes:Gasterosteidae) in Amory Cove, Quebec. Can. Fld. Nat. 87: 113-122.

Cone, D. K., and P. M. Ryan. 1984. Population sizes of metazoan parasites of brook trout (Salvelinus fontinalis) and Atlantic salmon (Salmo salar) in a small Newfoundland lake. Can. J. Zool. 62: 130-133.

Craig-Bennett, A. 1931. The reproductive cycle of the three-spined stickleback, Gasterosteus aculeatus L. Phil. Trans. Roy. Soc. Lond. B219: 197-279.

Dixon, W. J., and F. J. Massey, Jr. 1969. Introduction to statistical analysis. 3rd ed. McGraw-Hill: 638 p.

English, K. K. 1983. Predator-prey relationships of juvenile chinook salmon Oncorhynchus tshawytscha feeding on zooplankton in in situ enclosures. Can. J. Fish. Aquat. Sci. 40: 287-297.

Garside, E. T., and T. Hamor. 1973. Meristic variation in the threespine stickleback, Gasterosteus aculeatus L., in eastern Canadian waters. Can. J. Zool. 51: 547-551.

Greenbank, J., and P. R. Nelson. 1959. Life history of the threespine stickleback, Gasterosteus aculeatus Linnaeus, in Karluk Lake and Bare Lake, Kodiak Island, Alaska. Fish. Bull. Fish. Wildl. Serv. U.S. 59: 537-559.

Hanek, G., and W. Threlfall. 1970. Parasites of the threespine stickleback (Gasterosteus aculeatus) in Newfoundland and Labrador. J. Fish. Res. Board Can. 27: 901-907.

Hoffman, G. L. 1967. Parasites of North American freshwater fishes. Univ. Cal. Press. 186 p.

Jamieson, A. 1974. A water quality atlas for streams and lakes of insular Newfoundland. Fish. Mar. Serv. Data Rep. No. NEW/D-74-4. 22 p.

Jones, J. W., and H.B.N. Hynes. 1950. The age and growth of Gasterosteus aculeatus, Pygostius pungitus and Spinachia vulgaris, as shown by their otoliths. J. Anim. Ecol. 19: 59-73.

Laurent, P. J. 1972. Lac Leman: effects of exploitation, eutrophication, and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 867-875.

Maitland, P. S. 1965. The feeding relationships of salmon, trout, minnows, stone loach and three-spined sticklebacks in the River Endrick, Scotland. J. Anim. Ecol. 34: 109-133.

Mann, R.H.K. 1971. The populations, growth and production of fish in four small streams in southern England. J. Anim. Ecol. 40: 155-190.

Munzing, J. 1959. Biology, variability and genetics of Gasterosteus aculeatus. Investigations in the Elbe River region. Int. Rev. Ges. Hydrobiol. Hydrog. 44: 317-382. In German.

Narver, D. W. 1966. Pelagial ecology and carrying capacity of sockeye salmon in the Chignik lakes, Alaska. Ph.D. Thesis. Univ. of Washington, Seattle, Wash. 348 p.

Penczak, T. 1962. The stickleback (Gasterosteus aculeatus L.) from Nova Scotia, Newfoundland and the French island of Saint-Pierre. Ann. Zool. 20: 335-341. In Polish.

Pennycuick, L. 1971. Quantitative effects of three species of parasites on a population of three-spined sticklebacks, Gasterosteus aculeatus. J. Zool. Lond. 165: 143-162.

Pepper, V. A. 1976. Lacustrine nursery areas for Atlantic salmon in insular Newfoundland. Fish. Mar. Serv. Res. Dev. Tech. Rep. 671. 61 p.

Ryan, P. M. 1980. Fishes of the Lower Churchill River, Labrador. Fish. Mar. Serv. Tech. Rep. 922: vii + 189 p.

1982. Species composition and seasonal abundance of zooplankton in the Experimental Ponds Area, central Newfoundland, 1977-80. Can. Data Rep. Fish. Aquat. Sci. 318: iv + 85 p.

1984. Fyke net catches as indices of the abundance of brook trout, Salvelinus fontinalis, and Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. 41: 377-380.

Ryan, P. M., and D. Wakeham. 1984. An overview of the physical and chemical limnology of the Experimental Ponds Area, central Newfoundland, 1977-82. Can. Tech. Rep. Fish. Aquat. Sci. 1320: v + 54 p.

Scott, W. B., and E. J. Crossman. 1964. Fishes occurring in the fresh waters of insular Newfoundland. Dep. Fish. Ottawa. 124 p.

1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: ix + 966 p.

Tesch, F. W. 1971. Age and growth, p. 98-130. In W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. 2nd ed. Int. Biol. Prog. Handbook No. 3. Blackwell Scientific Publications, Oxford. 348 p.

Threlfall, W. 1968. A mass die-off of three-spined sticklebacks (Gasterosteus aculeatus L.) caused by parasites. Can. J. Zool. 46: 105-106.

Van Vliet, W. H. 1970. Shore and freshwater fish collections from Newfoundland. Nat. Mus. Nat. Sci. (Ottawa) Publ. Zool. 3. 30 p.

Wootton, R. J. 1976. The biology of the sticklebacks. Academic Press, London. x + 387 p.