AN ECOLOGICAL STUDY OF THE CESTODE *SCHISTOCEPHALUS SOLIDUS* IN THE THREE-SPINED STICKLEBACK, *GASTEROSTEUS ACULEATUS*, AT MATAMEK LAKE, QUEBEC.

by

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A thesis

submitted to the

Faculty of Graduate Studies and Research

in partial fulfilment

of the requirements for the degree of

Master of Science

Institute of Parasitology,

McGill University,

Montreal, P.Q.

ECOLOGY OF *SCHISTOCEPHALUS* IN THREE-SPINED STICKLEBACKS

ABSTRACT

A freshwater population of three-spined sticklebacks, Gasterosteus aculeatus, in northern Quebec, was sampled at regular intervals during the ice-free season over a two year period. From size frequency distributions it was estimated that sticklebacks at Matamek Lake live for at least three years. The majority of females matured when they were three years old. Breeding occurred in June and early July.

The 1+ age class of sticklebacks was most heavily infected with plerocercoids of Schistocephalus soidus. Infection levels increased from July to October and then dropped dramatically over the winter. Parasite abundance varied between 1981 and 1982. Schistocephalus was found to retard host growth, and maturation in females, and it appears that selective mortality of infected sticklebacks occurred over the winter. Few plerocercoids lived for more than one year. Plerocercoid growth was monitored and found to be density-dependent.

ABREGE

Une population lacustre d'épinoches à trois épines (Gasterosteus aculeatus), du nord du Quebec, a été échantillonnée durant la période de dégel, pendant deux années consécutives, à des intervals réguliers. D'après les courbes de captures il semble que l'espérance de vie des épinoches du lac Matamek soit d'au moins trois ans; âge auquel la majorité des femelles atteignent la maturité sexuelle. La période d'accouplement a lieu en juin et au début de juillet.

Les épinoches d'âge 1+ soit les plus fortement infestés par des plérocercoides de Schistocephalus solidus. Le niveau d'infestation a Schistocephalus solidus augmente de juillet à octobre, pour ensuite diminuer considérablement au cours de l'hiver. L'abondance du parasite au sein de la population d'épinoches varie entre 1981 et 1982. Schistocephalus semble retarder la maturation des épinoches femelles, ainsi que la croissance des individus en général. Les individus trés infestés seraient les plus susceptibles de mourir au cours de l'hiver. Trés peu de plérocercoides survivent plus d'une année. L'effet de la densité de l'infestation sur la croissance des plérocercoids est decrit.

SUGGESTED SHORT TITLE:

ECOLOGY OF *SCHISTOCEPHALUS* IN THREE-SPINED STICKLEBACKS

ACKNOWLEDGEMENTS

I would like to extend my sincere thanks to the following people:

Dr. M.A. Curtis for his advice and guidance during the course of the study and the preparation of the thesis.

My associates and friends at the Institute of Parasitology for their patience and assistance.

The staff at Matamek Research Station, especially Allan McNeill, for help in the collection of sticklebacks.

Brian Coad of the National Museum of Natural Sciences, Ottawa, for his advice and assistance.

Beth Crawford for so promptly coming to my assistance and typing the first draft of this thesis.

Joan Kearvell and Lesley Thompson for their help with the grahics.

April Kusek and Mary LaDuke for typing the tables.

Michel Berube for translating the abstract into French.

Marion Rigby and Joan Kearvell for the last minute checking for errors.

Last, but by no means least, all those who offered me their friendship and support during my stay in Sainte Anne-de-Bellevue.

Financial support was provided by a scholarship from the Science and Engineering Council, Swindon, England.

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CHAPTER I - INTRODUCTION

For many years parasite ecology was largely restricted to the description of parasite life cycles; however, over the last two decades parasitologists have become increasingly aware of the importance of a detailed knowledge of parasite and host ecology to the solution of parasitological problems. Many of the advances made in ecology have resulted from the formalization of ideas and concepts into theoretical models which have been tested using field and laboratory data. Parasitologists have begun to employ similar methodology in the study of host-parasite systems, but progress has been hindered by the paucity of integrated quantitative information available in the literature.

The aim of the present investigation was to describe, in detail, the interaction between the cestode, Schistocephalus solidus and its intermediate fish host, Gasterosteus aculeatus, under natural conditions. Seasonal studies of this association have been carried out on populations from England (Pennycuick, 1971a-d) and British Columbia (Peacock, 1979). It was considered that by obtaining a precise description of the relevant life history sequences of both the host and parasite under the different environmental regime offered in Quebec, and comparing findings with data from previous experimental and field studies, it would be possible to achieve a greater understanding of how the hosts and parasites interact under natural conditions.

In the following pages the reader is introduced to

some of the literature on G. aculeatus and S. solidus. It becomes immediately apparent that many aspects of the biology of these two species are extremely well documented. Thus, it has been necessary to be selective in reviewing previous works.

THE HOST - the three-spined stickleback, Gasterosteus aculeatus Linnaeus 1758.

Class - Osteichthyes

Subclass - Actinopterygii

Super Order - Teleostei

Order - Gasterosteiformes

Family - Gasterosteidae

The three-spined stickleback is found in marine and freshwater coastal habitats in the cold and temperate zones of Europe, North America and parts of Asia. Some populations are essentially marine, migrating into freshwater to spawn, while others live a completely freshwater existence exhibiting short migrations from deep water into the shallows at the onset of the breeding season (van Mullem and van der Vlugt, 1964). The geographical distribution of freshwater Gasterosteus aculeatus reflects the marine origin of this species and may be explained in terms of immigration from the sea (Munzing, 1963).

Throughout its distribution the three-spined stickleback exhibits extensive morphological, physiological and behavioural variation. Although the differences between some morphological

forms are known to have a genetic component (Heuts, 1947; Munzing, 1959; Lindsey, 1962; Hagen, 1967) it is not known to what extent the observed heterogeneity throughout the range of the species is a product of environmental variation and/or underlying genetic variation. Thus, the systematics of G. aculeatus remains a problem (Miller and Hubbs, 1969; Hagen and McPhail, 1970; Wootton, 1976). In recent literature three-spined sticklebacks are generally characterized as belonging to one of three morphological forms, or "morphs", termed leiurus, trachurus and semiarmatus (after Munzing, 1959), on the basis of the number and arrangement of lateral plates; however, these classifications are not used in any taxonomic or subspecific sense. The sympatric existence of different morphological forms at many locations has led several authors to examine the meristic variation exhibited by these sticklebacks (Heuts, 1947; Lindsey, 1962; Munzing, 1963; Hagen, 1967; Narver, 1969; Coad, 1972; Aneer, 1973; Coad and Power, 1974) and to compare the biology of different morphs in an attempt to examine the isolating mechanisms and processes of natural selection operating on these populations (Hagen, 1967; McPhail, 1969; Hagen and Gilbertson, 1972; Moodie, 1972b; MacLean, 1974; Moodie and Reimchen, 1976; Gilbertson, 1980; Hagen et al., 1980; Bell and Richkind, 1981). Until the relationships between inter- and intra- population variation and environmental constraints are understood, several authors maintain that the entire complex of morphs should be treated as belonging to a single highly variable species, Gasterosteus aculeatus L. (Miller and Hubbs, 1969; McPhail and Lindsey, 1970; Gilbertson, 1980).

The biology of the three-spined stickleback is extremely well documented. This is largely because of the abundance of this small fish in shallow, slow moving waters where it is readily observed and collected, and the ease with which it may be kept and bred in the laboratory. In particular, the peculiar reproductive behavior of the species has stimulated exhaustive ethological studies and the reproductive physiology is also remarkably well documented for a species of little commercial value.

The following account of the reproduction of the freshwater three-spined stickleback is taken from Wootton's (1976) review of the biology of sticklebacks.

Outside of the breeding season the stickleback lives in schools. At the onset of the reproductive phase mature males move into the shallows and establish a territory where they build a nest. Intruding male sticklebacks and other fish species are aggressively confronted and chased out of the territory. When a gravid female, recognizable by her distended abdomen, enters the territory the male and female commence a courtship ritual, as a result of which the female is enticed into the nest where she deposits her eggs. The female then leaves and the male fertilizes the eggs. A male may induce several females to spawn in the nest. He then adopts a parental role and tends to the young until they disperse. Males may build several nests and females may spawn several times during the breeding season. Post spawning mortality is common in this species, but some fish may survive and migrate into deeper water for the winter to return and breed again the following spring.

In a series of experiments, Baggerman (1957, 1972) studied the influence of photoperiod and temperature on maturation of sticklebacks from several annual, anadromous populations in Holland. A behavioural rather than histological criterion of sexual maturity was used; maturation was indicated by nest-building and egg laying in males and females respectively. On the basis of her experiments and field collections, Baggerman concluded that there were four phases in the development of sexual maturity in sticklebacks. Phase 0 was characteristic of juvenile fish collected in June and July (the first two months of life). These fish did not mature when kept under conditions of sixteen hours of light per day (16L8D) and 20°C. In contrast, fish in phase 1 would mature if kept under a similar light and temperature regime. These fish could be separated into two groups: fish in phase 1a showed an acceleration in the rate of gonadal maturation when kept under a photoperiod of eight hours light and sixteen hours of dark (8L16D) and at low temperature (4°C), whereas sticklebacks in phase 1b showed no such response. All fish in phase 1 could be kept sexually immature by maintaining them under a constant regime of 8L16D and 20°C. Sticklebacks in phase 1 were found in the field from August to late winter/early spring. Phase 2 fish became mature on a regime of 8L16D and 20°C, as well as on 16L8D and 20°C. This phase lasted from early spring until the start of the breeding season. Baggerman suggests that the phases correspond to changes in an annual cycle of an internal threshold to maturation; gonadal development to the next phase will only ensue when environmental conditions are suitable to

overcome the threshold. Thus, maturation is prevented at times of the year when production of offspring would be unfavourable to the survival of the species. Proposed histological equivalents to the phases in females are as follows: phase 0 corresponds to the initial period of oogenesis found in juvenile fish usually less than 22mm long; phase 1 corresponds to the growth and definition of the oocytes and the initial stage of yolk formation; whilst phase 2 includes the completion of vitellogenesis and final maturation of the oocytes (Baggerman, 1972; Wootton,1976).

It seems probable that maturation is similarly controlled in sticklebacks from populations which have a longer life span and which mature at the end of their first and subsequent years of life. However, it is not known how gonadal development proceeds in stickleback populations in which the fish do not mature until two or three years old.

In late summer and early autumn, the ovaries account for about 2% of the total body weight, this increases to about 4% in the early winter. During the breeding season the ovaries account for between 8 and 30% of the total body weight, depending on how recently the female has spawned (Meakins, 1974a, Wootton, 1976). In males the testes have become fully differentiated and contain most of the stages of spermatogenesis by the time the male is 25mm long. Maturation is accompanied by an increase in the proportion of body weight attributable to the testes (Wootton, 1976).

The variations in the spawning times of different populations of Gasterosteus aculeatus are reviewed by Freeman

(1965) and Coad (1972). In general, the breeding season commences earlier and is longer at temperate latitudes than at the subarctic and arctic parts of the species range. The findings of ecological and life history studies on the species with regard to the life span and age at maturity are tabulated in the next chapter.

The studies carried out on sticklebacks are reviewed extensively in Wootton's (1976) book, "The Biology of the Sticklebacks", and an updated bibliography of the Gasterosteidae is given by Coad (1981).

For the sake of brevity the three-spined stickleback, Gasterosteus aculeatus L. is referred to as "the stickleback" henceforth in this thesis.

THE PARASITE - Schistocephalus solidus (Müller 1776)

Class - Cestoda

Subclass - Eucestoda

Order - Pseudophyllidea

Family - Diphyllobothridae

Schistocephalus solidus is reported to occur throughout the geographical range of freshwater populations of Gasterosteus aculeatus: in the USSR (Dubinina, 1957; Bykhovskaya-Pavolovskaya et al., 1964 (cited by Wootton, 1976)), Europe (Clarke, 1954; Vik, 1954; Haitlinger and Wolanska, 1965; Vidal Celma, 1966; Arme and Owen, 1967; Chappell, 1969a; Pennycuick, 1971a) and in North America (Greenbank and Nelson,

1959; Freeman, 1965; Lester, 1969; Hanek and Threlfall, 1970; Coad, 1972; Peacock, 1979; Gilbertson, 1980; Reimchen, 1982).

Since Smyth (1946, 1950) described a technique for the cultivation and maturation of plerocercoids of Schistocephalus in vitro this parasite has been the subject of numerous experimental studies which have contributed to our knowledge of cestode physiology and biochemistry (Smyth, 1969).

Life history studies on Schistocephalus have been carried out by several authors (Dubinina, 1947; Smyth, 1947; Hopkins and Smyth, 1951; Clarke, 1954; Orr and Hopkins, 1969). The life cycle may be briefly summarized as follows: the adult worm is found in the intestine of a piscivorous bird. The adult parasite and eggs are passed out in the faeces within 1 to 3 days after the bird has eaten an infected stickleback. The eggs take 2 to 5 weeks to hatch, depending on the prevailing water temperature, and motile hexacanth larvae (coracidia) are released. These free swimming larvae may live for about 5 days. If eaten by one of several closely related copepods, the coracidium penetrates the intestinal wall of the copepod and enters the haemocoel. Multiple infections of procercoids in the coelomic cavity of copepods may occur. The infected copepod must be eaten by a stickleback for further transmission to be effected. In a matter of hours, the contained parasites may penetrate the gut wall and come to lie in the perivisceral cavity of the fish. Here they develop into plerocercoids capable of infecting bird hosts. The plerocercoids may live and continue to grow as long as their stickleback hosts.

The structure and life cycle of this cestode present

several unusual features. First, the adult parasite is not very host specific. At least 50 species of birds are recorded as being suitable definitive hosts (Freeman, 1965). In Canada these include guillemots, sandpipers, gulls, loons, mergansers, arctic terns, ravens and crows. In contrast, the plerocercoids of Schistocephalus are specific to sticklebacks. Dubinina (1959) recognized separate species of Schistocephalus infecting different fish hosts. There are several reports of the occurrence of S. solidus in fish species other than three-spined sticklebacks (Bangham and Adams, 1954; Dubinina, 1957; Hoffman, 1967; Lester, 1969; Dartnall, 1973; Margolis and Arthur, 1979). However, the experimental evidence presented by Braten (1966) and Orr et al. (1969) shows that Schistocephalus solidus is highly specific to Gasterosteus aculeatus and that this parasite does not become successfully established in other fish hosts.

Another striking attribute of this parasite is the extensive somatic growth and development exhibited by the plerocercoid in the stickleback. The characteristic complete external and internal segmentation and well developed genital primordia seen in plercercoids of Schistocephalus are unusual among cestodes and are only approached by the pseudosegmentation of the plerocercoid of Ligula intestinalis (Smyth, 1949). Because of these unusual characteristics, plerocercoids of Schistocephalus have been the subject of a series of experimental in vitro and in vivo growth and maturation studies (Hopkins and McCaig, 1963; McCaig and Hopkins, 1963; McCaig and Hopkins, 1965; Sinha and Hopkins, 1967; Orr and Hopkins, 1969; Meakins and Walkey, 1973).

THE ECOLOGY AND PATHOLOGY OF SCHISTOCEPHALUS IN GASTEROSTEUS

The most extensive studies on natural populations of sticklebacks infected with Schistocephalus are described by Pennycuick (1971a-d) and Arme and Owen (1967) in the UK and Freeman (1965) and Peacock (1979) in North America. In some stickleback populations parasite prevalence values apparently approach 100% at certain times of the year (Arme and Owen, 1967; Lester, 1969; Pennycuick, 1971a). Infections of Schistocephalus in Gasterosteus are overdispersed (Pennycuick, 1971c), the majority of parasites occurring in relatively few hosts. Multiple infections are common and the weight of the parasitic burden may be greater than the net weight of the host (Arme and Owen, 1967). Plerocercoids from multiple infections are reported to be smaller than those found in single infections (Vik, 1954; Orr and Hopkins, 1969; Lester, 1971), which implies that intraspecific competition may be occurring. Abdominal distension is characteristic of heavily infected sticklebacks.

It is suggested that Schistocephalus may cause or contribute to host mortality under natural conditions (Vik, 1954; Threfall, 1968; Pennycuick, 1971d). Cyclic fluctuations in the abundance of Schistocephalus and sticklebacks have been reported (Arme and Owen, 1967; Pennycuick,1971a). Pennycuick (1971d) suggests that both the parasite and host populations are regulated by parasite induced mortality. Infection with Schistocephalus increases stickleback mortality rates under normal laboratory conditions (Peacock, 1979) and to a greater extent in stressed mortality experiments, when the fish are

subjected to low oxygen and high temperature conditions (Peacock, 1979) or starvation (Walkey and Meakins, 1970; Pascoe and Mattey, 1977; Pascoe and Woodworth, 1980). Sublethal levels of Schistocephalus are reported to affect host growth (Pennycuick, 1971d), reproduction (Freeman, 1965; Arme and Owen, 1967; Meakins and Walkey, 1970; Pennycuick, 1971d; Coad, 1972; Meakins, 1974a), respiration (Lester, 1971; Meakins, 1974b; Meakins and Walkey, 1975), feeding (Freeman, 1965), behaviour (Arme and Owen, 1967; Lester, 1971; Coad, 1972; Giles, 1983), swimming ability and vulnerability to predation (Clarke, 1954; Arme and Owen, 1967; Coad and Power, 1973; Meakins, 1974a).

Hopkins and Smyth (1951) suggested that plerocercoids of S. solidus are eliminated from their stickleback hosts, thus accounting for the inverse relationship between the level of infection and host age seen in the population they studied. Vik (1954) observed plerocercoids of Schistocephalus "crawling through the body wall" of live sticklebacks trapped in water (25°C) in an abandoned boat, and there are other incidental references to plerocercoids rupturing the body wall of their hosts and sticklebacks having perforated abdominal walls (Hoffman, 1958; Freeman, 1965) . Live plerocercoids are occasionally observed free in the water (Vik, 1954; pers. obs.), however, experimental evidence suggests that sticklebacks are unable to survive such a trauma (Lester, 1969) and it is probable that worm emergence is a post-mortem response. Vik (1954) also reported finding dead and encysted plerocercoids in the abdominal cavity of three-spined sticklebacks and inferred that these plerocercoids had been neutralized by some host

immune response. Studies by Bråten (1966) and Orr et al. (1969) indicate that an immune reaction may be responsible for the destruction of plerocercoids in unsuitable hosts, however, to date there is no evidence that Gasterosteus aculeatus exhibits any such reaction to Schistocephalus solidus. Thus it is assumed that elimination of plerocercoids of S.solidus from this stickleback host does not occur (Pennycuick, 1971d).

RATIONALE

The widespread distribution and common occurrence of S. solidus in G. aculeatus have resulted in numerous records of this association in the literature. In many instances the reports are limited in detail because the investigators were primarily concerned with some other aspect of stickleback biology, or with surveying the entire parasitofauna of the host species or several host species.

As previously mentioned, a considerable amount of attention has been paid to the pathological effects of Schistocephalus on three-spined sticklebacks, and information regarding the seasonal changes in overall prevalence and intensity are available. However, few authors have concurrently integrated the relevant life history sequences and population dynamics of the host and parasite to the level of detail crucial to the understanding of how S. solidus and G. aculeatus interact in the field.

The evidence suggests that Schistocephalus solidus has

the potential to influence host population dynamics through effects on host survival, reproduction and behaviour, and that the parasite population dynamics may be regulated by parasite induced host mortality and intraspecific competition between parasites. Since the pathological effects of plerocercoids of S. solidus on three-spined sticklebacks are apparently mediated by competition for host energy resources, it seems probable that these effects would be exhibited to different extents among stickleback populations depending on environmental conditions.

In the present investigation, a population of three-spined sticklebacks from northern Quebec, Canada, was sampled at regular intervals over a two year period to attain the following objectives:

1. Provide a detailed description of the relevant life history sequences and population dynamics of Gasterosteus aculeatus and Schistocephalus solidus at this locale.

2. Fill gaps in our knowledge of this association by:

A. Monitoring the seasonal progress of plerocercoids, following aquisition, to obtain some estimate of in vivo growth and longevity of plerocercoids in the field.

B. Examining the effect of plerocercoids on sexual maturation in females separately for each age class, because sticklebacks do not necessarily mature in their first year of life (as has been assumed by several authors) and infection levels vary with host age.

3. Integrate the findings of the study with experimental evidence and data derived from field studies on populations from other locales with the ultimate aim of increasing our

understanding of how Schistocephalus solidus and Gasterosteus aculeatus interact under natural conditions.

The results of the present investigation are given in Chapters IV and V. In Chapter IV data regarding the life history of the host at the study area are presented. This provides the background for Chapter V in which the characteristics of infection with S. solidus are described. The findings are discussed in relation to other relevant literature at the end of each section. The results are summarized together with a few concluding remarks in the final chapter.

CHAPTER II - THE STUDY AREA

DESCRIPTION OF MATAMEK LAKE

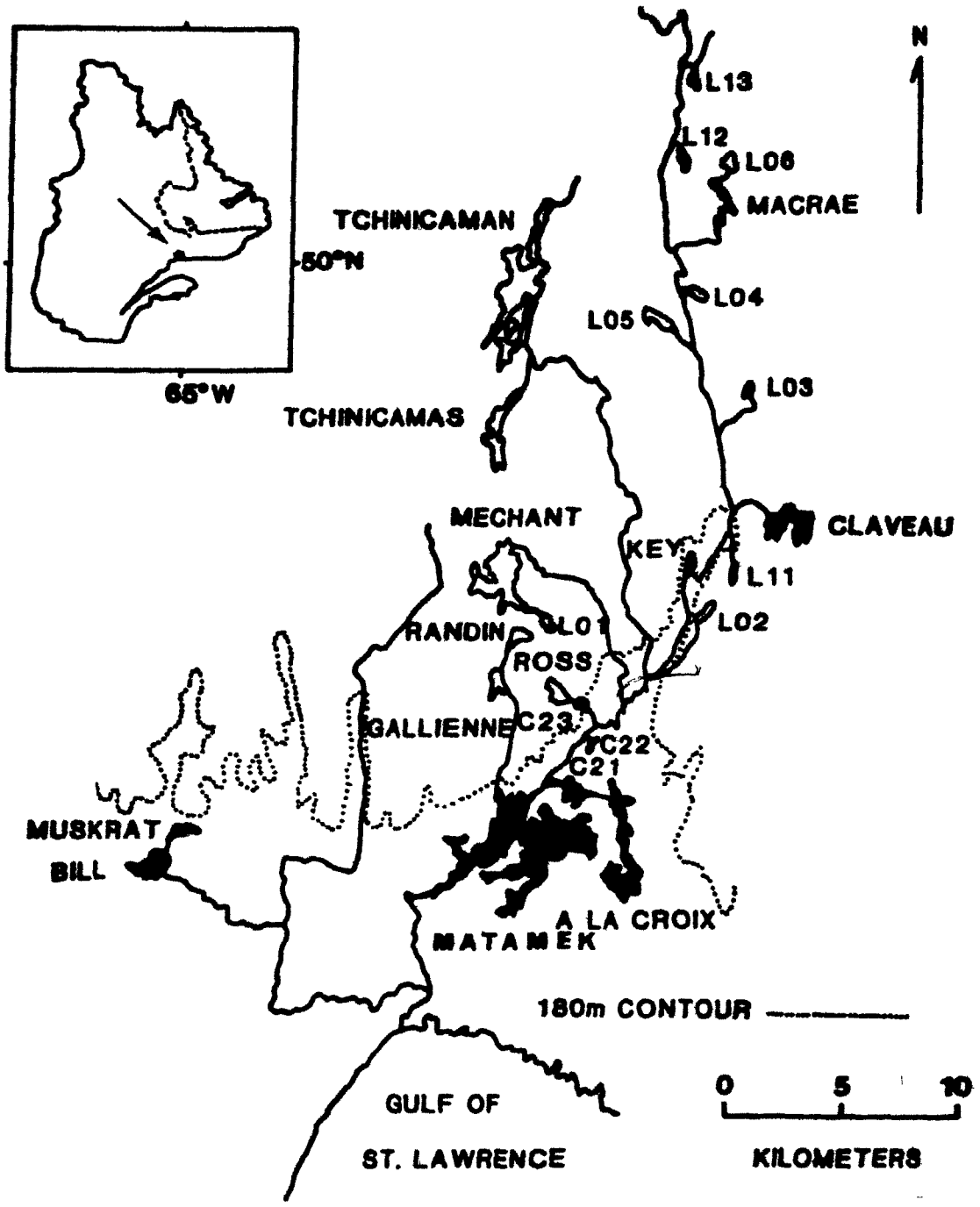
Matamek Lake (50°22' N, 65°54' W) is situated about 6.5 km inland from the north shore of the Gulf of St. Lawrence approximately 32 km east of the city of Sept-Iles, Saguenay County, Quebec. This lake, and the other lakes and rivers which constitute the Matamek Watershed are shown in Figure 1.

Matamek Lake lies at an elevation of 122 km, has a surface area of approximately 5.6 km^2 and a maximum depth of 100 m. As is characteristic of lakes in the area, Matamek Lake is oligotrophic (Saunders, 1969). The shorelines are generally steep and frequently rocky. Littoral vegetation is limited to a sparse narrow band encompassing a depth interval of approximately 3 m (Kreamer, 1980).

The thermocline reaches its maximum depth at approximately 10 m in mid to late August. Bottom temperatures are nearly always less than 8°C, and below 30 m are generally uninfluenced by circulation events and remain at temperatures of 4-5°C (Kreamer, 1980). During the winter the lake is covered by ice approximately 1 m thick. Breakup occurs in May, all ice leaving the lake by early June. Surface temperatures closely follow the surrounding air temperatures, reaching a maximum of 20°C in mid-summer. Cooling is gradual in the fall; the first signs of ice appear on the lake in late October (present study) and freeze-up occurs in December (Saunders, 1969).

The physiographic and limnological characteristics of the

Figure 1. The Matamek Watershed and its location in the province of Quebec, Canada (inset). Lakes containing fish are shaded and fishless lakes are unshaded.


N
L13
L12
L06
MACRAE
TCHINICAMAN
50°N
L04
L05
L03
65°W
TCHINICAMAS
MECHANT
CLAVEAU
KEY
L11
L02
RANDIN
L01
ROSS
GALLIENNE
C23
C22
C21
MUSKRAT
BILL
A LA CROIX
MATAMEK
180m CONTOUR
0
5
10
GULF OF
ST. LAWRENCE
KILOMETERS

lake are described in detail by Kreamer (1980). Meteorological data for 1967 is given by Saunders (1969) and temperature profiles of Matamek Lake are described by Saunders (1969), Pope (1973) and Janus (1976).

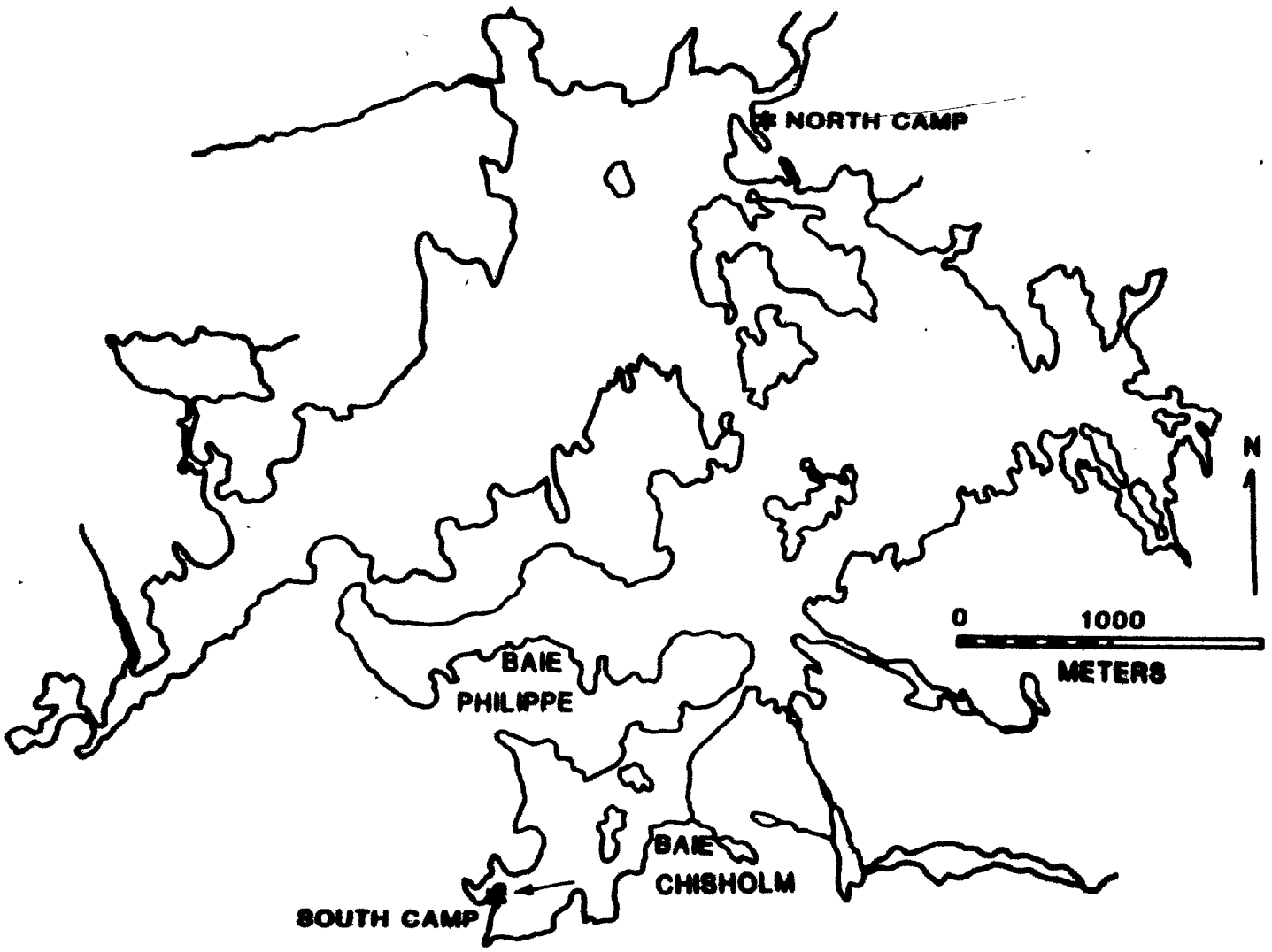
Matamek Lake contains five fish species: three-spined sticklebacks (Gasterosteus aculeatus), nine-spined sticklebacks (Pungitius pungitius), brook trout (Salvelinus fontinalis), arctic char (Salvelinus alpinus) and rainbow smelt (Osmerus mordax). The ecology and meristic variation of both species of stickleback are described by Coad (1972) and a survey of the parasitofauna of fish species in the watershed was carried out by Hanek and Molnar (1974). Information is also available regarding the trout, char and smelt (Saunders, 1969), macrozoobenthos (Kreamer, 1980), zooplankton (Pope, 1973) and phytoplankton (Janus, 1976) communities in the lake. The flora and fauna of the surrounding area are described by Saunders (1969).

DESCRIPTION OF THE SAMPLING STATIONS

Samples of three-spined sticklebacks were collected at two locations at Matamek Lake. These collection areas lie in close proximity to the cabins situated on the north shore of the lake and on a small peninsula of the south shore at Baie Chisholm and are henceforth named the North camp and the South camp respectively. (See Figure 2)

The sampling area at the North camp extended along

Figure 2. Outline of Matamek Lake showing the location of the two sample sites, the North camp and the South camp.


NORTH CAMP
N
0
1000
METERS
BAIE
PHILIPPE
BAIE
CHISHOLM
SOUTH CAMP

approximately 50 m of shoreline, immediately in front of the encampment, encompassing a maximum depth interval of approximately 1 m. For the greater part of the sampling season the substratum of this area was composed of sand interspersed by small stretches of rocks. In the spring and autumn, when the water level was high, a higher proportion of the sampling area was made up of rocks. Littoral vegetation was very sparse, however, some additional shelter was provided by occasional submerged logs.

The shoreline immediately in front of the South camp was steep and composed of rocks sloping sharply down to depths of several meters. Consequently, seine nets could not be used in the collection of sticklebacks at this site. Sampling using dip nets was also restricted because of the steep incline.

HISTORY OF THE MATAMEK WATERSHED

The present distribution of fishes in the Matamek Watershed may be attributed to the effects of the Wisconsin Glaciation (Power et al., 1973). The Labradorian ice sheet effectively eliminated all species of freshwater fish from the land mass north of the Gulf of St. Lawrence. Following the retreat of the ice, parts of the present land surface became submerged beneath the Champlain Sea, which reached a height of 128 m above the present sea level and extended 9 km inland from the modern coastline (as far as Key Lake, see Figure 1). As a result, the lakes and rivers of the Champlain Plain were

colonized by euryhaline species of fish. Subsequently, the fish species of these waters became isolated from the sea by the series of waterfalls and rapids found down the length of the Matamek and Muskrat Rivers. Colonization of the waters beyond Key Lake was limited due to the rapids and waterfalls of the Upper Matamek River, formed as a result of the drop in elevation from the Laurentian Plateau (Coad, 1972, Power et al., 1973). The number of fish species present at any location in the watershed decreases progressively from the mouth of the Matamek River to the headwaters. The distribution of species in the system indicates the order in which these species arrived in the system (Power et al., 1973).

CHAPTER III - MATERIALS AND METHODS

FIELD METHODS

Three-spined sticklebacks were collected from Matamek Lake at regular intervals during the ice free periods from July 1981 to June 1983, providing a data base of almost 2,500 fish. The sampling dates, number of fish per sample, collection methods and sample sites are shown in Table 1. Dip nets (mesh 1mm) and seine nets (mesh 6mm) and plastic and galvanized wire minnow traps (maximum mesh 5mm) were employed in the study. The use of minnow traps proved to be the least efficient method because catches were always very low; however, they were used in all the sampling carried out at the South camp to supplement the numbers collected by dip net, which was also of limited success at this location because of restricted access to the shoreline. Seine nets could not be used at the South camp because of the steep incline, but this method proved to be highly successful in the shallows at the North camp. Since infected sticklebacks are readily visible from the water surface it was considered that samples collected using dip nets would be biased in favour of infected fish, consequently, seine nets were employed almost exclusively at the North camp; dip nets were only used to collect fry which were able to escape through the mesh of the seine.

The sticklebacks were preserved in 70% alcohol because

Table 1. Capture data for three-spined sticklebacks from Matamek Lake, Quebec. 1981-83.

Date	Sample site	Sample size	Collection methods
9-10.7.81	South Camp	175	Dip net & minnow trap
01.8.81	South Camp	66	Dip net & minnow trap
16.8.81	North Camp	167	Dip net, minnow trap & seine
18.8.81	South Camp	151	Dip net & minnow trap
28.8.81	South Camp	198	Dip net & minnow trap
11-13.9.81	North Camp	511	Seine
29-30.10.81	North Camp	230	Seine
16.6.82	North Camp	100	Seine
30.6.82	North Camp	149	Seine
14.7.82	North Camp	160	Seine
28.7.82	North Camp	92	Seine
11.8.82	North Camp	164	Seine
25.8.82	North Camp	208	Seine & dip net*
12.6.83	North Camp	150	Seine

* Dip net only used in collection of stickleback fry.

LABORATORY METHODS

The length from the snout to the tip of the central caudal fin ray (fork length) of each fish was recorded to the nearest millimetre.

A small lateral incision was made in the abdominal wall of each fish and the entire ventral surface was cut away, including the pectoral girdle, exposing the body contents from the anus to the lower jaw. Large plerocercoids were eased out of the body cavity using blunt forceps. The cavity and intact viscera were then washed well with 70% alcohol to remove any small plerocercoids. The alimentary canal was cut at the anus and at the base of the lower jaw and removed. The gonads were removed and, where possible, sexed. (In the young of the year it was frequently not possible to differentiate between the two sexes.) Ovaries from the July 1983 sample were classified as being immature or mature. Immature gonads were recognized as containing numerous semi-transparent, white, equally sized oocytes. Mature gonads showed variously sized oocytes, some opaque due to vitellogenesis, and fully developed yellow eggs. Spent ovaries, recognized by their relatively large size and thick walls, were also included in this category. The body cavity was again examined for parasites and the kidney tissue was scraped out using a blunt spatula. This entire process was carried out in 70% alcohol in a petri dish under a binocular microscope.

The roof of the skull of each fish was sliced off, the brain displaced and the sagittae (the largest pair of otoliths)

were removed. (For specific details, see Jones and Hynes, 1950). The otoliths were kept in 70% alcohol until needed. Then they were transferred in pairs into absolute alcohol for several minutes, cleaned in creosote for another 5 minutes and mounted in Permount^{R} (Fisher Scientific Company, Fair Lawn, New Jersey, U.S.A.). Each pair was examined by reflected light against a dark background, to facilitate the counting of the annulations which indicate fish age, on three independent occasions. Several hundred pairs of otoliths from several different samples were examined in this way.

The eviscerated fish, gonads and individual worms were all transferred into separate vials or trays and dried in a drying oven at 70^{o}C for 48 hours. (In an earlier trial, fish, gonads and worms were weighed at several time intervals after being put in the drying oven; it was found that even the largest fish gave consistent dry weight readings well within this 48 hour limit). The dried specimens were then weighed to the nearest 1/10th of a mg on a Mettler AC88 Delta Range^{R} balance (Mettler Instrument Corporation, Hightstown, New Jersey, U.S.A.).

Wet weights (after blotting) of the eviscerated fish, gonads and plerocercoids were also recorded for fish collected in June 1983, so that the relationship between dry and wet weights could be established.

Since plerocercoids of Diphyllobothrium spp. may also be found in the perivisceral cavity of Gasterosteus aculeatus (Vik, et al., 1969) and Diphyllobothrium is reported to occur in other fish species at Matamek Lake (Hanek and Molnar, 1974), all

plerocercoids, especially the smaller ones, were examined closely to ensure that plerocercoids of Diphyllobothrium were not mistaken for plerocercoids of Schistocephalus. In addition, the gut and associated viscera were examined superficially for cysts of Diphyllobothrium spp. No cysts or plerocercoids were ever observed.

STATISTICAL METHODS

Data analysis was carried out using the Statistical Analysis System (SAS), a software package of the McGill University Computing Centre. Described in detail by publications of the SAS Institute Inc. (1982a, 1982b), the system includes routines for subsetting data, tabulating frequency distributions, and running statistical tests. The original data remain on file at the Institute of Parasitology of McGill University.

To separate individual fish into age classes on the basis of their size, polymodal analysis, after the method of Cassie (1954), was carried out by plotting the length frequency data for each sample on probability paper. In most cases the distribution was not unimodal (as indicated by a straight line on the graph paper), but bimodal or trimodal (shown by two or three curves connected by points of inflexion). Each component curve was replotted on probability paper and a straight line (the best fit of the points, as judged by eye) was drawn through the points (see Figure i, Appendix). To minimize the

possibility of including fish in the wrong age class, it was decided that only those fish lying within the 90% confidence limits of each cohort would be included in that cohort in later analyses. The implications of such discrimination are discussed later.

The Parasite Index (P.I.) described by Arme & Owen (1967) was calculated for each infected fish.

$$P.I.\% = \frac{\text{Total worm dry weight}}{\text{Fish dry weight + Total worm dry weight}} \times 100$$

The Gonadosomatic Index (G.I.) described by Meakins (1974a) was calculated for all females.

$$G.I.\% = \frac{\text{Dry weight of gonads}}{\text{Dry weight of fish}} \times 100$$

In the following chapters the terms prevalence, intensity, mean intensity and abundance, employed in the description of the infection of Gasterosteus aculeatus with Schistocephalus solidus are used in accordance with the definitions described by Margolis et al. (1982).

CHAPTER IV - THE LIFE HISTORY OF THE THREE-SPINED STICKLEBACK AT MATAMEK LAKE.

INTRODUCTION

The life span and growth of sticklebacks have been determined for several populations at different localities in Europe (Bertin, 1925; Jones and Hynes, 1950; van Mullem and van der Vlugt, 1964; Mann, 1971; Pennycuick, 1971b; Wootton et al., 1978) and in North America (Greenbank and Nelson, 1959; Freeman, 1965; Coad, 1972; Moodie, 1972a; Gilbertson, 1980). The reported life span varies from one to five years and growth rates also apparently vary between populations (Coad, 1972; Wootton, 1976). All authors are in agreement that spawning occurs in the spring (Jones and Hynes, 1950; Wootton, 1976), however, the age at which sticklebacks reach maturity also varies between populations, and males and females from a given population may mature at different ages (Freeman, 1965). Since post spawning mortality is a relatively common phenomenon in this species it follows that the age at which sticklebacks spawn may be related to the life span of a given population.

Some of the observed variations in the life histories of different populations of sticklebacks may be attributed to genetic differences between populations, but environmental influences are of obvious importance because growth and maturation of this species are largely dependent, whether directly or indirectly, on photoperiod and temperature.

to affect growth, maturation and survival in sticklebacks (Pennycuick, 1971d) and infection levels vary between locations, the presence of this parasite may also contribute to some of the differences in stickleback life history observed among stickleback populations.

In this chapter the life history of Gasterosteus aculeatus at Matamek Lake is described and compared to the life histories of stickleback populations from other locations. The relationships between the level of infection with plerocercoids of Schistocephalus and the ovarian development and growth of specific age classes of sticklebacks are described and discussed.

RESULTS

The results of age determination from otolith readings were highly inconclusive. In less than 50% of instances were the readings consistent through all three trials. Reading of the otoliths was complicated by their extreme variability, which was exhibited in centrum size and composition, whether or not the centrum was banded, centrum opacity, band width and opacity. Even the outermost band varied from being transparent to opaque in fish from the same sample. Otoliths from many of the largest fish were so thick and rough on the surface that bands were not apparent at all. Considering the low success rate it was considered that age estimation by this method was unreliable for this series of samples.

The length frequency distributions of sticklebacks in each sample are shown in Figure 3A. It can be seen that several samples were comprised of 2 or 3 distinct cohorts of fish. By following the growth of fish in a given cohort through one growing season to the next it was apparent that these cohorts represented age classes. Polymodal analysis of the data indicated which modes could be separated on a statistical basis. In most cases the overlap between successive modes in the length frequency distributions was restricted to the extreme ends of each component normal distribution. As described in the Materials and Methods, only those fish lying within the 90% confidence limits of each cohort were considered as belonging to a given age class in subsequent analyses. Weight frequency distributions were compiled to assist in the determination of the age composition of the samples. A cube root transformation was used to normalize the weights on a scale comparable to that used in the length frequency distributions. The weight frequency distributions are shown in Figure 3B. It may be seen that the same modes emerge as in Figure 3A. On the basis of these frequency distributions, it is estimated that three-spined sticklebacks at Matamek Lake live for at least three years. The mean lengths and 90% confidence limits for each cohort derived from polymodal analysis and the inferred age of each cohort are given in Table 2. Young of the year are designated 0+, fish which have lived through one, two and three (or more) winters are designated 1+, 2+ and 3++ respectively.

Prior to the collection of the last sample of sticklebacks in June 1983, a life span of two years and some

Figure 3. Size frequency distributions for three-spined sticklebacks collected at Matamek Lake, 1981 - 1983.

A. Length frequency distributions.

B. Weight frequency distributions.

Sample sizes are given in Table 1.

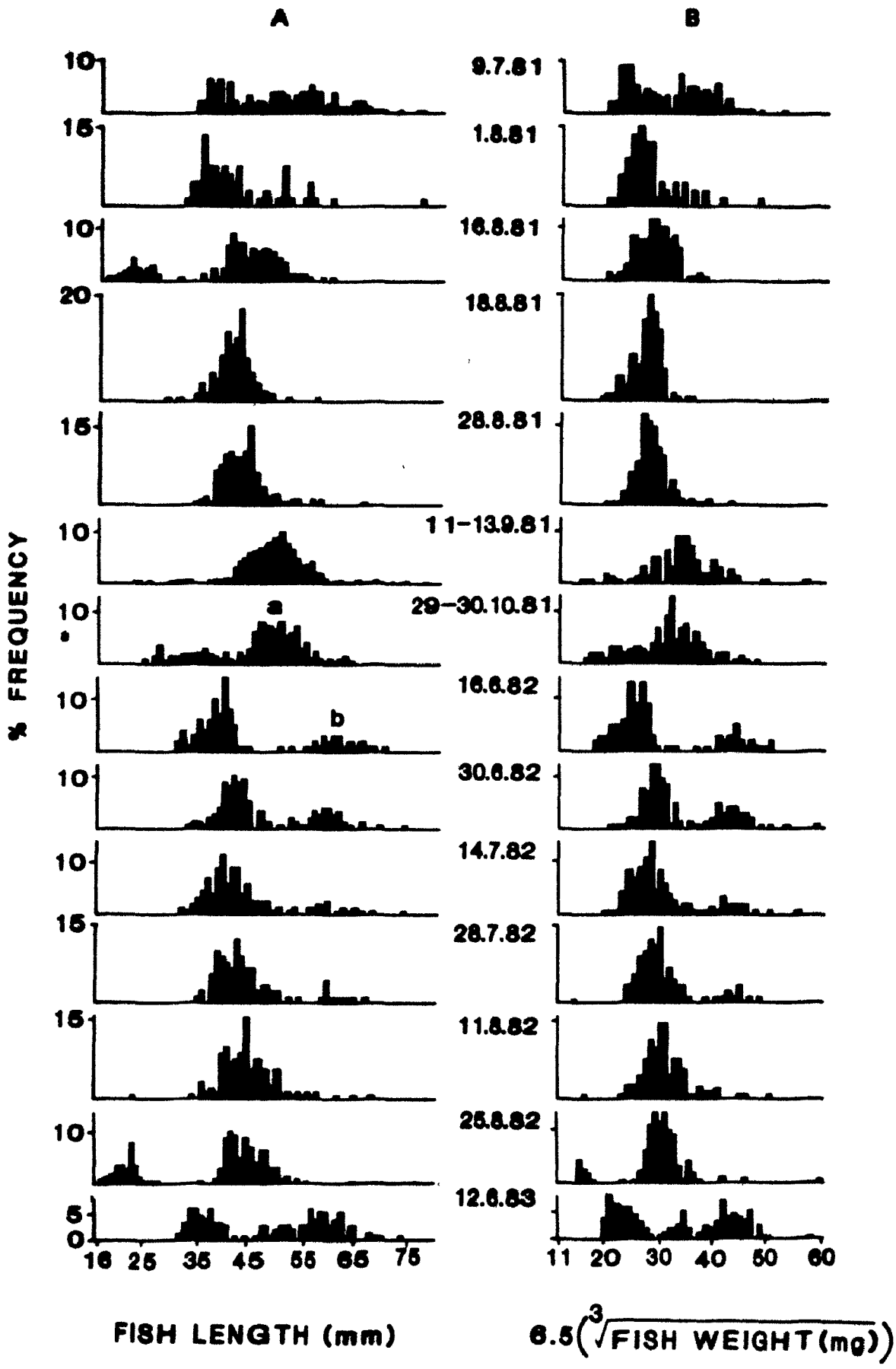

A
B
% FREQUENCY
9.7.81
1.8.81
16.8.81
18.8.81
28.8.81
11-13.9.81
29-30.10.81
16.6.82
30.6.82
14.7.82
28.7.82
11.8.82
25.8.82
12.6.83
a
b
16 25 35 45 55 65 75
11 20 30 40 50 60
FISH LENGTH (mm)
6.5(∛FISH WEIGHT(mg))

Table 2. Inferred ages, minimum and maximum lengths and mean lengths of sticklebacks in cohorts derived from polymodal analysis of length frequency distributions, (fish with lengths outside the 90% confidence limits of each component normal distribution are excluded).

Date	Number of fish in cohort	Age	Fork length (mm)		
			Minimum	Maximum	Mean
16.8.81	33	0+	18	26	22.5
	117	1+	38	52	43.6
11-13.9.81	8	0+	23	32	29.2
	435	1+	42	56	48.8
29-30.10.81	50	0+	27	39	33.2
	143	1+	45	55	49.3
16.6.82	63	1+	32	41	36.6
	24	3++	52	67	60.5
30.6.82	89	1+	36	45	41.7
	43	3++	52	64	58.2
14.7.82	121	1+	35	47	40.7
	21	3++	56	67	60.5
28.7.82	71	1+	38	48	42.0
	10	3++	59	66	60.5
11.8.82	133	1+	37	49	43.4
	10	3++	54	67	57.4
25.8.82	53	0+	18	25	21.3
	139	1+	40	51	44.0
12.6.83	52	1+	32	39	35.5
	13	2+	47	51	49.6
	62	3++	55	66	59.8

months was considered because of the bimodality of the size frequency distributions of samples collected in October 1981 and June and July 1982. However, on the basis of this interpretation it was difficult to account for the size discrepancy between the 1+ sticklebacks in October 1981 (indicated by "a" in Figure 3A), which had a mean fork length of 49.8mm and a mean dry weight of approximately 140mg, and the cohort of larger sticklebacks collected the following June (indicated by "b" in Figure 3A), which had a mean fork length of 60.7mm and a mean dry weight of approximately 310mg, if these fish all belonged to the same year class. It seems unlikely that sticklebacks could exhibit such a large growth increment over the cold winter months. It will be seen later that there is an inverse relationship between fish size and parasite burden. Sticklebacks in cohort "a" (see Figure 3A) were all infected whereas only 12.5% of those in cohort "b" (see Figure 3A) were infected, and it could be suggested that these fish represent the infected and uninfected components of the same cohort, however, the findings of the present study indicate that the weight difference between these two cohorts of sticklebacks was too great to be the product of parasitism alone, especially since the condition factors and thus the weights of sticklebacks are reported to decrease over the winter months in populations subjected to more favourable conditions (Pennycuick, 1971d; Wootton et al., 1978). The length and weight frequency distributions of the sample collected in June 1983 were trimodal. Since males and females were represented in all three cohorts, it was considered that three-spined sticklebacks at Matamek Lake may live for at least three years and some

months.

An interesting feature of the distributions is the apparent absence or scarcity of 2+ fish in 1982 and 1983. Although it was not possible to separate the July 1981 sample into component age classes, because of the presence of overlap between the modes in the length frequency distributions, the range of fish lengths and weights when compared with those of fish collected in 1982 suggests that the July 1981 sample was composed of 1+, 2+ and 3++ fish, the 2+ age class being well represented. A comparison of the length and weight frequency distributions for males and females from this sample (see Figure ii, Appendix) indicated that sexual dimorphism with respect to size may have been partially responsible for the overlap. Thus, polymodal analysis was carried out independently for the two sexes, but, no clear delineation of age classes was exhibited. No significant differences in fish length or weight were found between the two sexes within any other cohort of fish. However, in the 3++ age class mean lengths and weights of females were always greater than those of males, and all 8 of the largest fish collected (mean fork length > 70 mm) were females. It should be noted that the prior use of 90% confidence limits on fish length distributions to delineate the constituent age classes would serve to decrease any apparent differences in size between the two sexes.

Various characteristics of sticklebacks (aged 1+) collected at the North camp and South camp on 16.8.81 and 18.8.81 respectively were compared to see if the samples from both locations could be combined seasonally. The results of the

Table 3. Results of a t-test comparing characteristics of two samples of three-spined sticklebacks (aged 1+), infected with *Schistocephalus*, collected at the North and South Camps of Matamek Lake on 16.8.81 and 18.8.81 respectively.

Characteristic	p
Stickleback length	0.0004
Stickleback weight	0.0001
Parasite intensity	0.1636
Parasite Index	0.0014

North Camp, n = 117

South Camp, n = 135

t-test are shown in Table 3. Mean fish lengths and weights and the Parasite Indices of the sticklebacks from the two locations were significantly different, consequently only data from the sticklebacks collected at the North camp were used to examine stickleback growth.

A composite growth curve for this population of sticklebacks is presented in Figure 4. The growth rate is most rapid in the young of the year and decreases as the fish get older.

The relationship between the fish dry weight and the Parasite Index of 1+ sticklebacks collected in September 1981 is shown in Figure 5. This sample was selected to examine the effects of plerocercoids of Schistocephalus on stickleback growth because it contained more fish than any other, and infection levels were high at this time of year. The fish dry weight decreases significantly with increasing levels of parasitaemia. The relationship is described by the linear equation:

Stickleback dry weight (mg) = 249.6 - 2.9(P.I.%)

$p < 0.0001$ $n = 434$

$r = 0.667$

Stickleback length is also inversely correlated to the Parasite Index (raw data not shown), but the association exhibits greater scatter; the relationship is described by the equation:

Stickleback fork length (mm) = 54.7 - 0.2(P.I.%)

$p < 0.0001$ $n = 434$

$r = 0.522$

Figure 4. Growth curve for three-spined sticklebacks collected at the North camp of Matamek Lake. The curve is compiled from the mean fork lengths of sticklebacks of age classes derived from polymodal analysis of the length frequency distributions. Data from all three years is included. ○ - 1981. ● - 1982. △ - 1983. Numerical values are given in Table 2.

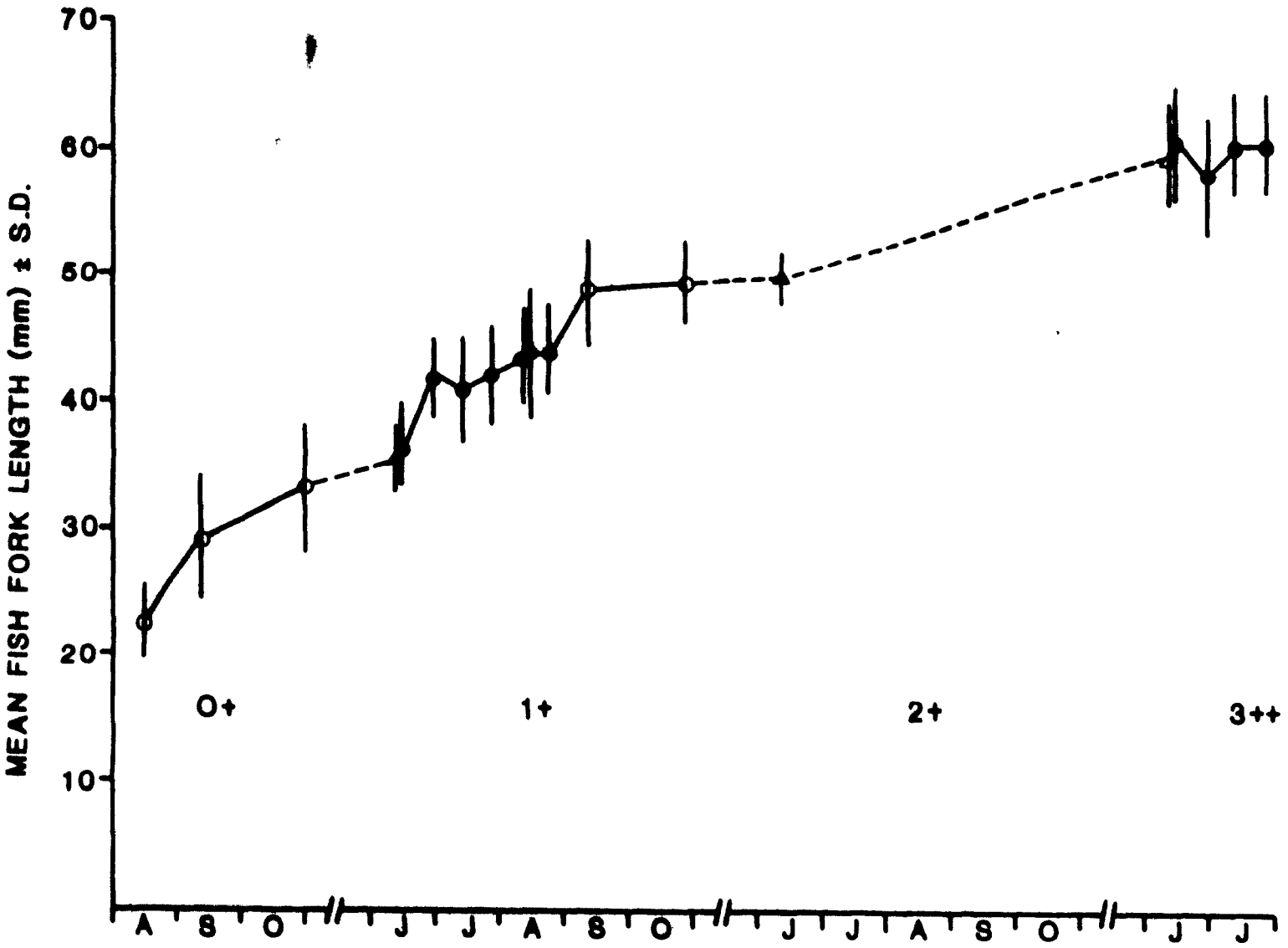
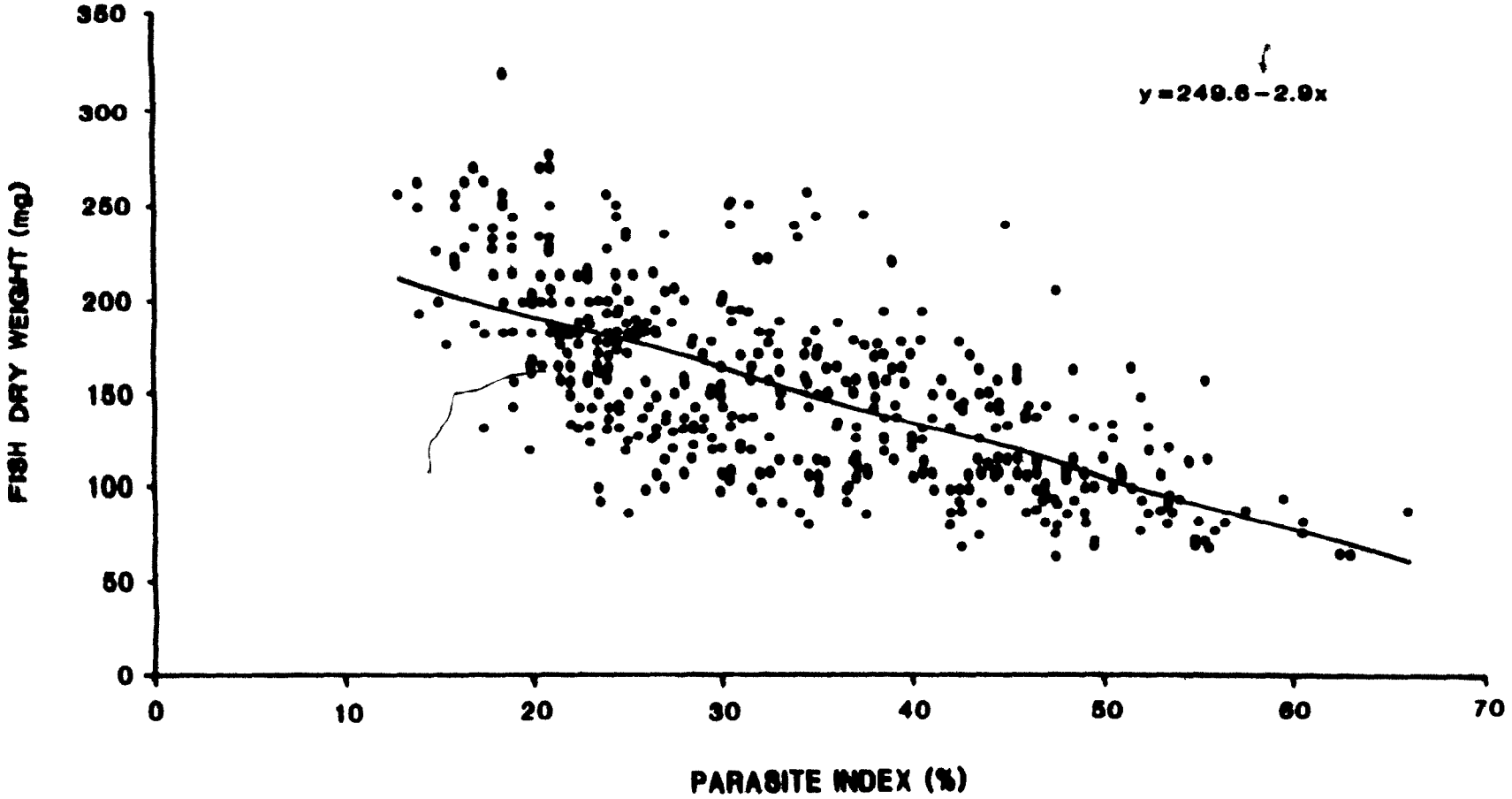

MEAN FISH FORK LENGTH (mm) ± S.D.
70
60
50
40
30
20
10
0+
1+
2+
3++
A
S
O
J
J
A
S
O
J
J
A
S
O
J
J

Figure 5. The relationship between the weight of G. aculeatus and the Parasite Index for 1+ sticklebacks collected in September 1981.


y=249.6-2.9x
FISH DRY WEIGHT (mg)
350
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
PARASITE INDEX (%)

For comparative purposes, the same equations were calculated for sticklebacks (aged 1+) collected in October 1981:

Stickleback dry weight (mg) = 232.8 - 2.0(P.I.%)

$p < 0.0001$ $n = 143$

$r = 0.574$

Stickleback length (mm) = 53.2 - 0.1(P.I.%)

$p < 0.0003$ $n = 143$

$r = 0.300$

The frequency distributions of Gonadosomatic Indices (G.I.) of different age classes of females from all samples are given in Figure 6. Females having G.I. values between 8 and 33% were collected in June and July in all three years indicating that breeding occurs during this period. A single female with a G.I of 45% was found in late August, 1981. Examination of the ovaries of the fish revealed the occurrence of corpora aretica indicating that it had failed to spawn; this fish was infected with S. solidus (P.I.=21%). From Figure 6 it is apparent that in the majority of cases females do not reach maturity until they are three years old. The classification of females, collected in June 1983, as either mature or immature on the basis of the gross morphology of their ovaries confirmed this finding (see Figure 7). With the exception of one 2+ fish, which measured 51 mm (see Table 2 for maximum and minimum lengths of fish included in each age class) and which had mature ovaries, 0+, 1+ and 2+ females had G.I. values below 2% throughout the sampling period, indicating that they were immature. Four 3+ females were immature, three of these were infected with

Figure 6. Frequency distributions of Gonadosomatic Indices for female sticklebacks, 1981 - 1983. Stickleback ages are indicated by shading. □ - age unknown. ■ - 0+. ▨ - 1+. ▧ - 2+. ■ - 3++. The asterix marks the female which had corpora atretica.

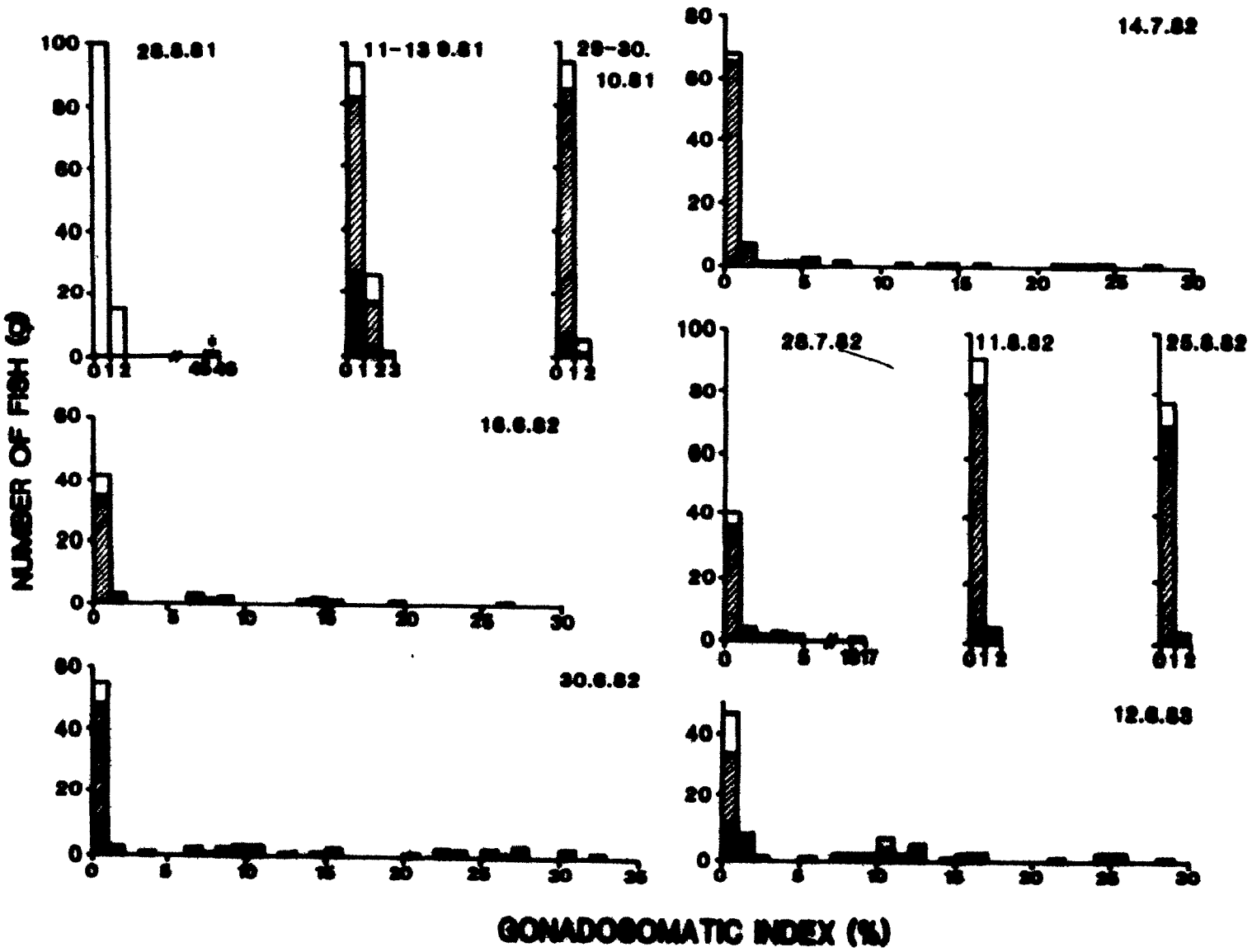
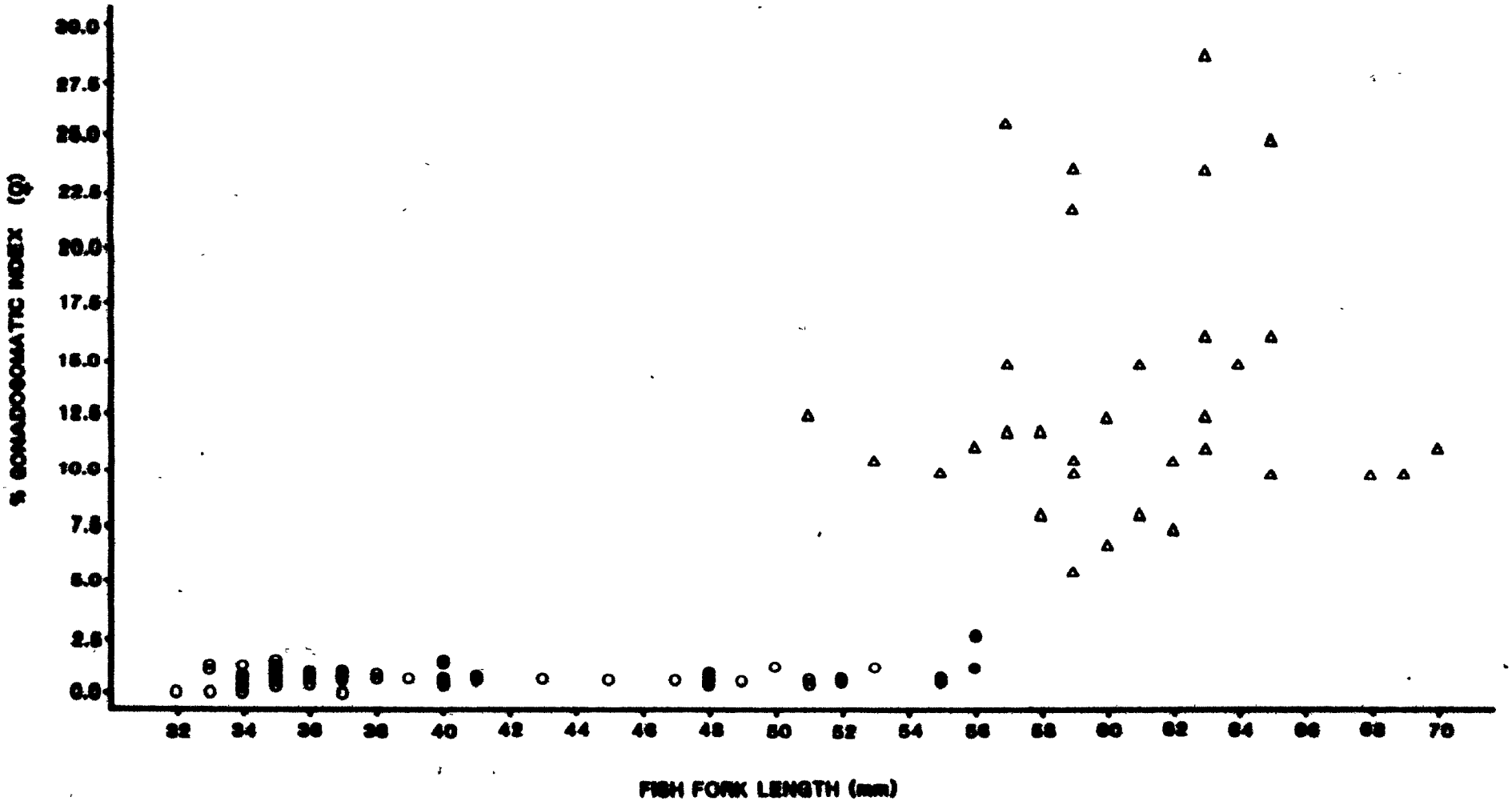

28.8.81
11-13 9.81
29-30. 10.81
14.7.82
16.8.82
28.7.82
11.8.82
25.8.82
30.8.82
12.8.83
NUMBER OF FISH (g)
GONADOSOMATIC INDEX (%)

Figure 7. The relationship between the Gonadosomatic Index, fork length, level of maturity and infection with S. solidus for female sticklebacks collected at the North camp in June 1983. ○ - immature. ● - immature and infected. △ - mature.


% GONADOSOMATIC INDEX (GI)
30.0
27.5
25.0
22.5
20.0
17.5
15.0
12.5
10.0
7.5
5.0
2.5
0.0
32
34
36
38
40
42
44
46
48
50
52
54
56
58
60
62
64
66
68
70
FISH FORK LENGTH (mm)

Schistocephalus. All other 3++ females had mature ovaries, the G.I. varying from 5 to 29% depending on how recently the female had spawned.

It was not feasible to determine the pattern of gonadal growth in males because the weights of the testes were generally too small to be measured reliably on the balance used.

Wet weight/dry weight conversion ratios for eviscerated sticklebacks, their ovaries and plerocercoids of Schistocephalus solidus, stored in 70% alcohol, are given in Table iv of the appendix.

DISCUSSION

The life span and age at maturity that have previously been determined for populations of sticklebacks are summarized in Table 4. The life span is reported to vary from one to five years and sticklebacks apparently reach maturity at different ages at different locales. Variations in the timing and length of the breeding season are also presented in Table 4. It appears that these variations are related to the temperature of the habitat; the spawning season commences earlier and continues longer in temperate environments than in the more northerly parts of the species range (Freeman, 1965; Coad, 1972). In many populations the aftermath of spawning is that all or most of the adults die (van Mullem and van der Vlugt, 1964; Hagen, 1967; Mann, 1971). In these populations the life span will be determined by the age at which the fish mature.

Table 4. Variations in normal life span, age at maturity and timing of the spawning season between freshwater stickleback populations. The methods used in age determination and the morph composition of each population are indicated where known.

Reference	Location	Normal life span (years)	Age at maturity (years)	Timing of spawning season	Method	Morph composition
Bertin (1925)*	France & Netherlands	1½	1	April-June	lfd	mixed
Bock (1928)*	Germany	3			lfd & o	leiurus
Munder (1930)**	Germany	3				trachurus
Craig-Bennett (1931)**	England	>2		late April-May		leiurus
Jones & Hynes (1950)	England	3½	1	April-May	o	leiurus
Greenbank & Nelson (1959)	Alaska, U.S.A.	2½	1	late May-early Aug.	lfd & o	leiurus
Freeman (1965)	N.W.T., Canada	5	2(m) 3(f)	mid June-early July	lfd & o	
Harvey (1969)	Alaska, U.S.A.	2	2	late June-early July		mixed
Mann (1971)	England	1½	1	begins in May	lfd & o	
Pennycuick (1971d)	England	3½		May-July	lfd & o	
Coad (1972)	Quebec, Canada	2½	2	June-July	lfd & o	semiarmatus
Moodie (1972a)	Queen Charlotte Islands, Canada	>2	>2(m)	May-July	lfd & o	leiurus & b
Ahnar (1973)	Sweden	4	2		lfd & o	mixed
Wootton et al. (1978)	Wales	1½	1	May-July	lfd & o	leiurus
Peacock (1979)	British Columbia Canada	2	1	June-July	lfd	
Gilbertson(1980)	Alaska, U.S.A.	>3	3	July	lfd & o	mixed
present study	Quebec, Canada	>3	3	June-July	lfd & o	semiarmatus

lfd - length frequency distribution
o - otolith reading
b - "black" sticklebacks, described by Moodie (1972a)
(m) - male
(f) - female

* cited by Jones & Hynes (1950) and Freeman (1965)
** cited by van Mullem and van der Vlugt (1964) and Freeman (1965)
Preferred methods used in age determination are underlined; in all cases these data are taken from the references cited, except for the information volunteered by Wootton (pers. comm.)

According to Baggerman (1972), the ability of a stickleback to respond to external stimuli and mature is more closely related to the attainment of a certain internal physiological state rather than a given age. Since growth and development are dependent on the rate of food assimilation, (Wootton, 1976) which in turn depends on food availability and environmental factors (Nikolskii, 1963), one would expect to find variations in the life span, age at maturity and the size of sticklebacks at different locations.

Gilbertson (1980) proposes that much of the observed variation in life span may be attributable to average climatic conditions. To support this hypothesis he compares the life span of three populations of sticklebacks studied at different latitudes on the west coast of North America; stickleback populations in Washington (Lat. 46-49^{o}N) generally live for one year, a population studied by Moodie (1972a) on the Queen Charlotte Islands, B.C. (Lat. 53^{o}N) lives for at least two years and that studied by Gilbertson at Lake Aleknagik (Lat. 59^{o}N) follows this trend and has a life span of three or more years. Greenbank and Nelson (1959) proposed a two and a half year life span for sticklebacks on Kodiak Island, Alaska (Lat. 57^{o}N). Gilbertson (1980) suggests that Greenbank and Nelson erred in their analysis of the results and that sticklebacks at this location may live for at least three years. Having examined the data presented by Greenbank and Nelson (1959), I concur with Gilbertson's interpretation. The comparison of life spans of other populations not considered by Gilbertson (1980) tends to favour his hypothesis, although it must be remembered that a

change in latitude does not necessarily imply a correlated change in climatic conditions because many other factors such as the size and the elevation of the water body inhabited determine the extent to which freshwater poikilotherms are subjected to climatic conditions. Bertin (1925), Mann (1971) and Wootton et al. (1978) reported populations of sticklebacks from France, southern England and mid-Wales respectively, as exhibiting life spans of just over one year. The population described by Jones and Hynes (1950), from a more northern location in England, and that studied by Pennycuick (1971a), from a pond, also in southern England, at a higher elevation than that studied by Mann, apparently live for a little over three years. (It should be noted that the populations studied by Pennycuick (1971a) and Wootton et al. (1978) were both found in water bodies at similar elevations.) Results of the present study indicate a life span of at least three years for sticklebacks in southern Quebec, Aneer (1973) found four year old sticklebacks in a population from Sweden and Freeman (1965) describes a subarctic population of sticklebacks from the Belcher Islands, N.W.T. as living for approximately five years.

Van Mullem and van der Vlugt (1964) maintain that the composition of each population with respect to morphs affects the life span. From the data presented in Table 4 there does not seem to be any direct correlation between the life span and morph composition of stickleback populations. However, considering the adaptive flexibility of this species from one location to the next it is probable that genotypic differences do contribute to the observed variability in life span.

The age at which Gasterosteus aculeatus matures also varies among populations (see Table 4). Sticklebacks may mature for the first time at the end of their first, second or third year of life. Globally speaking, sticklebacks from more northerly locations mature at a later age. The only apparently incongruous result is that given by Greenbank and Nelson (1959) who aged two year old fish as yearlings, however, this result should be viewed with caution since these authors also mistook renal tissue for gonadal tissue in a population they described as being hermaphroditic (Stenger, 1963).

Growth curves for stickleback populations compiled from the data presented by various authors are given in Figure 8. Although any conclusions based on specific comparisons of these curves should be regarded with some caution due to the heterogeneous nature of the origins of the data, some features of Figure 8 are of interest. Populations of sticklebacks from England apparently exhibit a higher growth rate during the first year of life, attaining a greater size at the end of a years growth than those from more northerly locations. It seems probable that growth during this period, when the growth rate is at a maximum, is strongly influenced by temperature. Under the more favourable conditions encountered in England sticklebacks may reach a suitable state of development in their first year to mature when a year old, and at a length of approximately 44 mm (Mann, 1971).

Freeman (1965) and Baggerman (1972) indicate that males may mature at an earlier age and smaller size than females. Freeman (1965) described males from the Belcher Islands as

Figure 8. Comparative growth curves for freshwater G. aculeatus. The curves were compiled from data given by the present and previous authors.

●—● Holloway (present study)

○—○ Coad (1972)

▲—▲ Gilbertson (1980)

△—△ Freeman (1965)

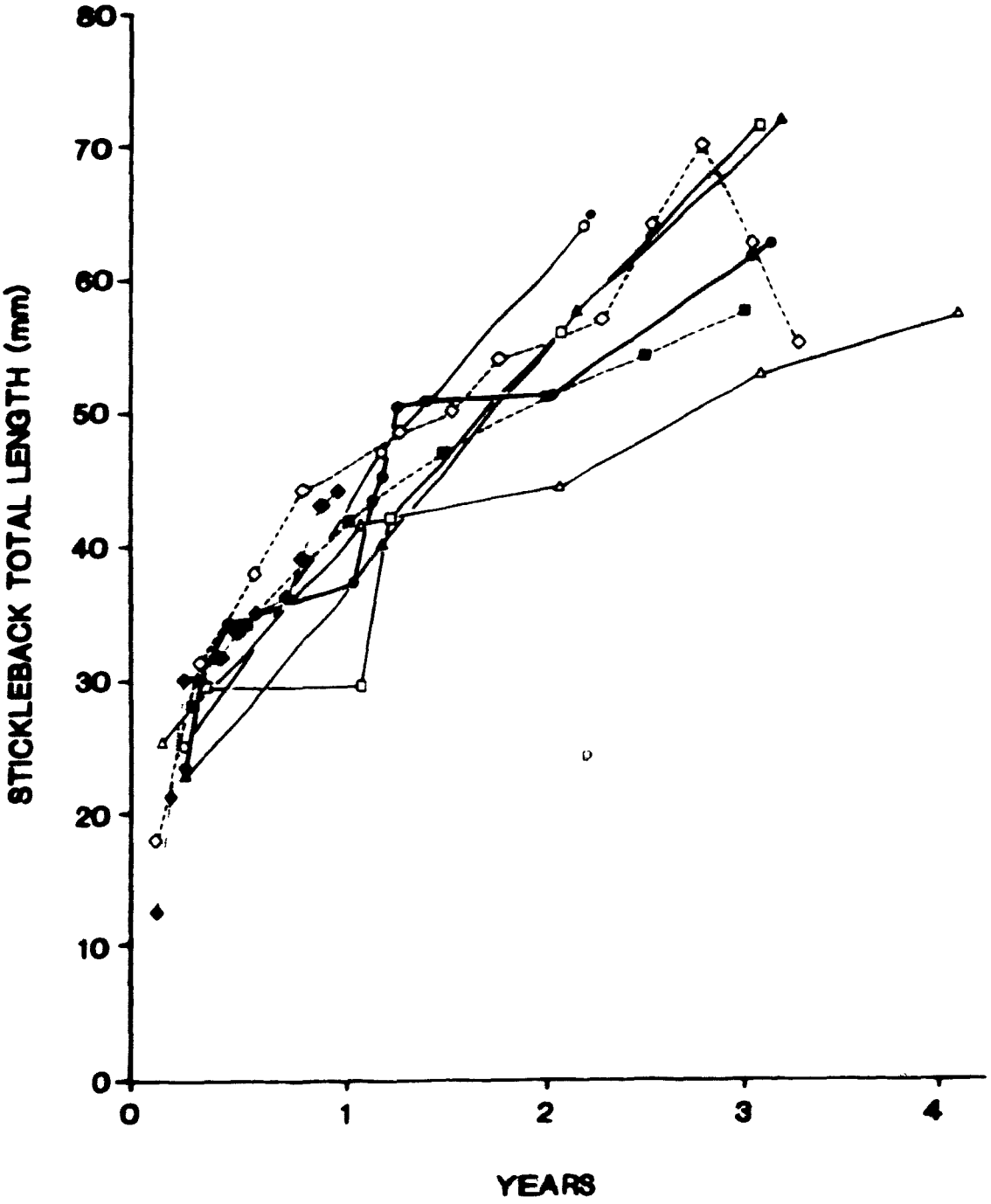
■—■ Pennycuick (1971d)

□—□ Greenbank and Nelson (1959)

◆—◆ Mann (1971)

◇—◇ Jones and Hynes (1950)

The asterix marks the mean fork length of Coad's designated 2+ year class (see text for details).


STICKLEBACK TOTAL LENGTH (mm)
80
70
60
50
40
30
20
10
0
0
1
2
3
4
YEARS

maturing when approximately 45 mm long; this is in agreement with the findings of Craig-Bennett (1931) (cited by van Mullem and van der Vlugt, 1964) and Mann (1971) from studies in the U.K. In the same study Freeman (1965) reported breeding to occur for the first time in females in a 50-55 mm length class. In the present study no females less than 51 mm were found to have mature ovaries.

In many populations there is sexual dimorphism in size, females of a given age being larger than males of an equivalent age. This phenomenon is most common in older fish (Greenbank and Nelson, 1959; van Mullem and van der Vlugt, 1964; Pennycuick, 1971b; Coad, 1972). In the present study, it appeared that sexual dimorphism in size occurred in fish collected in July 1981 at the South camp. It was not possible to quantify this observation because these fish could not be aged reliably. Statistical comparisons of the sizes between the sexes of fish of known age from the North camp did not show significant differences. However, the magnitude of any such differences would have been underestimated because the 10% of the fish at the extreme ends of the length distributions were omitted from the analyses.

The mean length of the oldest age class of sticklebacks is highly variable (see Figure 8) and does not appear to be directly correlated with environmental conditions. The maximum size attained by sticklebacks from a given population probably reflects some combination of environmental and genotypic differences. It is of interest that the population from the Belcher Islands, N.W.T., described by Freeman (1965), exhibited

the longest life span, late maturation and the slowest growth rate, since, of all the populations described here, this population was probably sujected to the most adverse conditions.

On reviewing the accounts presented by various authors regarding the life history of the three-spined stickleback, it becomes immediately apparent that there are problems encountered in comparing the data on sticklebacks beside the fact that these fish are genetically highly variable and exposed to a wide variety of environmental conditions. The methodology employed in the collection of sticklebacks and subsequent interpretation of data also vary from study to study.

For many years it has been common fisheries practice to age fish populations using polymodal analysis based on length measurements; the counting of rings on otoliths has only proven reliable for a few fish species. Bock (1928, cited by van Mullem and van der Vlugt, 1964) and Munzing (1959) examined the otoliths of freshwater and anadromous sticklebacks respectively and concluded that age determination by fish length was the preferable method. Munzing indicated that otolith reading was extremely unreliable because of the difficulty encountered in distinguishing successive rings. Jones and Hynes (1950) aged three populations and stated that they were able to read at least one of the two otoliths from each fish in over 99% of cases. They were unable to differentiate between age groups on a length basis because extensive overlap occurred between the length frequency distributions of successive age classes of sticklebacks. Consequently these authors maintain that otoliths provide the only accurate means of age determination in

sticklebacks, although they did describe the otoliths as being variable. Since then several authors (see Table 4) have attempted to determine the age structure of stickleback populations by both methods, with varying degrees of success. Gilbertson (1980) compared the results he obtained by otolith reading, statistical analysis of length frequency distributions and visual inspection of length frequency distributions. He found agreement among methods and concluded that age designation using length frequency distributions was the most efficient method because it took the least time. Moodie (1972a) reported that the otoliths he studied were very variable and that he was only able to obtain consistent readings from about 50% of the pairs he examined. In the present study the same problem was encountered. It was further noted that many of the otoliths from the largest fish were completely opaque. Freeman (1965) also had difficulties in ageing larger specimens collected from N.W. Hudson Bay whereas he was able to obtain consistent readings from 98% of sticklebacks collected from S.E Hudson Bay. Since the opaque layer is laid down in the winter it may be that the prolonged winters experienced by many stickleback populations in North America render the otoliths more opaque and make the intermittent bands less easily discernible. The deposition of an additional layer during the final winter of life may render the otoliths of the oldest fish completely unreadable. Coad (1972) and Greenbank and Nelson (1959) state that they only aged a subsample of their otoliths and it is possible that other authors did likewise. Under these circumstances the oldest age class may be completely overlooked.

It is on this premise that I question Coads' (1972) findings that sticklebacks at Matamek Lake, Quebec, live for just over two years. The mean length of Coad's designated 2+ year class (indicated by the asterix in Figure 8) is higher than that for 2+ sticklebacks at any other location. It may be that conditions were particularly favorable for stickleback growth prior to sampling in 1970 and that the sticklebacks were sufficiently large and well developed to mature in their third spring. Alternatively, and on the basis of the present findings, it is suggested that Coad's designated 2+ year class was composed of 2+ and 3+ fish and that sticklebacks at Matamek Lake may live for at least three years. Some may live for an additional year but a 4+ age class could not be distinguished on the basis of length frequency distributions.

Age determination on the basis of length frequency distributions also poses problems. In some populations overlap between the length frequency distributions of age classes is extensive (Jones and Hynes, 1950; Pennycuick, 1971d). Power (1965) suggests that the degree of overlap between the lengths of age classes is related to environmental conditions. Under more favourable conditions, growth of the young of the year is sufficiently rapid that overlapping age groups may occur after just a few months, while under more severe conditions overlapping of year groups may only occur between the older age groups. The extent of overlap is also likely to be greater for populations having a longer spawning season (Coad, 1972). It seems that the length frequency distributions provide a better indication of the life span of stickleback populations from

colder climates. Since growth rate decreases with age, care must be taken in the interpretation of these distributions, however, by examining the change in the length frequency distributions over extended time periods, this drawback may be largely overcome.

In the present study the 2+ age class appeared to be rare or absent in most samples with the exception of that collected in July 1981. This sample and two of the samples taken in August 1981 were collected at the South camp of Matamek Lake whereas all others were collected at the North camp (Table 1). The differences in the age composition of the samples taken in July 1981 and 1982 may reflect temporal variation in the strength of year classes; this phenomenon has been reported by Gilbertson (1980). Alternatively, this difference may reflect the differential spatial distribution of age classes within the lake. The absence or rare occurrence of an age class in a series of stickleback samples is not uncommon. The examination of the length frequency distributions for sticklebacks at Karluk Lake, Alaska (Greenbank and Nelson, 1959, Fig. 7) indicates that 2+ fish were absent from the sampling area from June through early August, reappearing in small numbers in late August and early September. Rogers et al. (1963) and Rogers (1968) (cited by Manzer, 1976) observed that "By midsummer, fish of age I and II became pelagic while age 0 and III tended to remain inshore". Such a distribution could feasibly be related to the territorial behaviour of adult males during the breeding season. Breeding males are known to be highly aggressive towards conspecifics of comparable size whereas they are tolerant of smaller

sticklebacks (van den Assem, 1967). The gentle gradient of the littoral zone at the seining site at the North camp makes it a suitable habitat for males to establish their territories and build their nests. The apparent scarcity of 2+ sticklebacks at this location may well be due to their being chased out of the seining area by territorial males. Even if 2+ males are physiologically able to spawn they are probably prevented from doing so by the larger dominant 3++ males.

In the current investigation only one 2+ female was found to be gravid. This fish was collected in June 1983, at a time when the 2+ class was poorly represented. 2+ fish were apparently absent from samples collected at the North camp during the breeding season in 1982, thus it is difficult to ascertain what proportion of 2+ females usually mature at Matamek Lake.

When given a choice of two dummy female sticklebacks of similar size, which differ only in their degree of abdominal distension (indicating that they are ready to spawn), sexually active male sticklebacks will preferentially choose the dummy with the more swollen belly as a mate (Rowland, 1982). There are several reports in the literature from studies on other fish species that show that breeding fish prefer larger mates (Hanson and Smith, 1967; Perrone, 1978; Downhower and Brown,1980). Since larger sticklebacks lay greater numbers of eggs at a given spawning than do smaller ones (Wootton, 1973), it would be advantageous for male sticklebacks to selectively mate with larger females. Under such circumstances, the larger, mature individuals of a given population would comprise the dominant

reproductive force, with smaller individuals making up the reserve in years when the older age classes are poorly represented. Since there is no evidence to support this hypothesis it is not possible to do more than speculate. However, the above interpretation could explain the relative changes in abundance of 2+ fish on the breeding grounds during the spawning season. Alternatively, very few 2+ sticklebacks may mature and their scarcity may simply be the result of aggression between conspecifics. 2+ fish were found in greater numbers at the South camp. The shoreline at this location does not offer suitable breeding substrate and shoals of 2+ fish may occur in such areas to feed. It is possible that a proportion of those fish measuring over 55 mm collected in September and October 1981 are representatives of the 2+ age class returning to feed and perhaps surviving 3++ sticklebacks may also be present (see Figure 3A). On the basis of the rather limited data available it appears that only a small proportion of 2+ females mature.

Although stickleback behaviour may account for the spatial distribution of sticklebacks in Matamek Lake, several recent studies on natural populations indicate that the situation may be even more complex. Gilbertson (1980) provides evidence that the sticklebacks within a lake may comprise not one population but several subpopulations exhibiting different characteristics and occupying restricted areas within the lake. Although the population at Matamek Lake is considered to be monomorphic with respect to lateral plate number (Coad, 1972) whereas that studied by Gilbertson (1980) at the Lake Aleknagik,

Alaska, was polymorphic with respect to lateral plate number, the spatial distribution of subpopulations described by Gilbertson was not correlated to this meristic characteristic. Larson (1976) describes a population of sticklebacks from a lake on Texada Island, British Columbia, as being composed of two phenotypes exhibiting differential spatial distributions, behaviour patterns, feeding habits and growth rates. MacLean (1974) studied a stickleback population from another lake on Texada Island and described it as being composed of residents which remain in a restricted area, maintain a breeding and feeding territory and non-residents which move from area to area and do not breed. MacLean maintains that this reflects the social hierarchy which exists within stickleback populations, the dominant sticklebacks being residents and the subordinates belonging to the roving group. Because the possession of a territory confers selective advantages on the holder with respect to feeding, survival and reproduction (MacLean, 1974), it follows that differences in fish size, fecundity and relative abundance of age classes may be apparent between the two groups.

Since the fish collected from the two sample sites in mid August had different mean lengths and weights, and sexual dimorphism in size was only obvious in sticklebacks from the South camp, it is feasible that the samples may have been collected from two different subpopulations. Consequently, samples from the two locations were not pooled in later analyses. Sex ratios were not calculated because spatial segregation of sexes is known to occur in this species (Gilbertson, 1980). These inter- and intra-population

differences again highlight the difficulties in comparing data on natural populations of sticklebacks. A sample collected at a specific location may not be representative of the population as a whole.

The timing of fish collection and the methods used may also affect the composition of any sample. In some populations diel changes in the mean size of sticklebacks occur in the littoral zone (Manzer, 1976). Sticklebacks are commonly collected using either dip nets, seines, or minnow traps, or some combination of these methods. Sticklebacks heavily infected with Schistocephalus solidus are readily visible from above because of the lateral displacement of their white ventral surfaces and they are easily caught (Clarke, 1954; Arme and Owen, 1967). As a result, dip netting and to a lesser extent seining are probably biased towards the collection of infected fish. Reimchen (1982) found that significantly higher percentages of fish infected with S. solidus occurred in collections made with a beach seine than with minnow traps during the same period. Since he does not indicate whether the traps were placed outside or within the seining area, it is not possible to determine whether this result reflects different levels of bias in the two methods towards catching infected fish or the spatial segregation of infected and uninfected sticklebacks in the lake. Minnow traps probably provide the least biased samples and have the advantage that they may be placed at any depth, however, frequently the catches taken in these traps are too low for them to be effective (Arme and Owen, 1967; the present author).

There are many reports that infection with S. solidus affects the reproductive development of G. aculeatus. Meakins (1974a) compared the Gonadosomatic Indices of infected and uninfected sticklebacks and found that during the breeding season the G.I. of uninfected fish was significantly higher than that of infected fish. In the autumn following the breeding season Arme and Owen (1967) and Meakins (1974a) found the situation reversed, infected fish having more ovarian tissue than uninfected fish. In the latter situation the ovaries of infected fish exhibited increased corpora atretica. This condition has been suggested to indicate that the fish were unable to spawn (Kerr, 1948). A female with a G.I. of 45% was found at Matamek Lake in late August 1981, well after the termination of the breeding season. This fish had a P.I. of 21% and had apparently failed to spawn. Freeman (1965) found that a P.I. of up to 7.5% had no discernable effect on the maturation of the ovaries whereas maturation was prevented in all females with a P.I. greater than 15%. The macroscopic examination of the ovaries from sticklebacks collected at Matamek Lake in June 1983, revealed that all designated 3++ females had mature ovaries with the exception of four fish which were immature, three of these females were infected with S. solidus. These fish had P.I.'s of 30, 25 and 25% respectively. All mature 3++ fish were uninfected.

Pennycuick (1971d) described a negative correlation between the developmental state of the gonads of both male and female sticklebacks and the P.I. and prevalence values. Arme and Owen (1967) and McPhail and Peacock (1983) reported similar

effects on ovarian development. All of these authors examined these relationships for all age classes collectively on the assumption that it is usual for Gasterosteus aculeatus to breed in its first year of life (based on the findings of Jones and Hynes (1950)). Since sticklebacks from some populations do not mature until they are two or three years old, and the level of infection commonly varies with host age (see next chapter for details), the relationship between infection levels and the state of reproductive development should be examined separately for each age class. Although the numbers of infected fish found during the breeding season at Matamek Lake were low, the data support the hypothesis that infection with S. solidus retards ovarian maturation in adult females (aged 3++). The G.I. values of 0+, 1+ and 2+ fish were virtually always less than 2% throughout the sampling season, regardless of the degree of infection.

In situations where maturation is completed in infected fish, egg number may be reduced (Coad, 1972; Meakins, 1974a). In mating experiments parasitized females, recognized as gravid by males due to the parasite induced abdominal distension, were mostly unreceptive to male courtship. The one female that responded destroyed the nest. In other instances the frustrated male either drove the female away or attacked and killed her. Grossly distended parasitized males were unable to construct nests (Arme and Owen, 1967; Meakins, 1974a).

Arme and Owen (1967) also looked for delayed gonad maturation in males. They did not find any pronounced or constant differences evident in gross or histological appearance

between the testes of infected and uninfected fish. McPhail and Peacock (1983) found no differences in infection levels between reproductive males and the population at large. In contrast, Freeman (1965) found the testes in heavily infected males to be smaller than those in uninfected males.

Ligula infections have similar, but more extreme effects on reproduction in roach (Rutilus rutilus), bream (Abramis brama) and dace (Leuciscus leuciscus). Even single infections result not only in retarded oogenesis but also in inhibition of spermatogenesis (Arme, 1968; Arme and Owen, 1968; Sweeting, 1976). Arme (1968) found that ligulosis in roach also produces changes in the host pituitary, in the cells responsible for producing gonadotrophins. In three-spined sticklebacks there is apparently no difference between the pituitaries of fish infected with Schistocephalus and uninfected fish (Kerr, 1948; Arme and Owen, 1967). Doyle (1978) studied Schistocephalus infections in the nine-spined stickleback (Pungitius pungitius), and found that Schistocephalus prevents spermatogenesis and vitellogenesis in this host, regardless of the degree of parasitism. Meakins (1974a) suggests that retarded ovarian maturation in three-spined sticklebacks results from the parasites competing directly with the host for available energy resources. This may account for the apparent lesser effect of the parasite on testicular development because egg production is far more expensive in terms of energy than spermatogenesis.

Schistocephalus is also reported to affect growth in sticklebacks (Lester, 1969; Pennycuick, 1971d). In the present study, a significant negative correlation was found to exist

between the dry weights and lengths, and Parasite Indices of infected 1+ sticklebacks, indicating that the parasites are responsible for the retardation of host growth. It was not possible to determine the effects of parasitism with S. solidus on the growth of older sticklebacks because these were largely uninfected. From the regression lines fitted to the data for 1+ sticklebacks collected in September 1981 it may be extrapolated that sticklebacks with a P.I. of 35% (the mean for the age class at this time of year) weigh 40% less and are 13% shorter than their uninfected counterparts. It is probable that these values are overestimates because the model requires that even very low levels of parasitaemia have a significant effect on fish growth. This may be the case during the winter months when food is scarce, but, 0+, and 1+ sticklebacks (which were all apparently infected) showed growth increments between September and October, implying that food availability was not limiting to growth at this time. Pennycuick (1971d) calculated the relationships between the intensity of parasitic infection and both condition factor (weight/length^3) and length. Using these relationships she calculated theoretical values of the condition factor, length and hence weight of uninfected fish. She estimated that in the period from August 1967 to April 1968, when the mean P.I. for all age groups fell between 30 and 35%, infected sticklebacks weighed, on average, 25% less than they would have if uninfected, and that the retardation of growth was more pronounced in older fish. Such retardation of growth as a result of infection with S.solidus may account for the differences in the size of sticklebacks from the two sample

sites in the present study, since 1+ fish collected at the South camp had a significantly lower mean weight and mean length and a significantly higher P.I. than those collected at the North camp.

The possible effects of Schistocephalus solidus on the population dynamics of Gasterosteus aculeatus are discussed in Chapter VI.

CHAPTER V - CHARACTERISTICS OF THE INFECTION OF *SCHISTOCEPHALUS SOLIDUS* IN THREE-SPINED STICKLEBACKS AT MATAMEK LAKE

INTRODUCTION

Seasonal variations occur in the infection patterns of *S. solidus* in *G. aculeatus* (Clarke, 1954; Freeman, 1965; Arme and Owen, 1967; Chappell, 1969a; Lester, 1969; Pennycuick, 1971a; MacLean, 1974; Peacock, 1979; Gilbertson, 1980; Reimchen, 1982) throughout the geographical range of this association. Infection levels are similar in the two sexes (Freeman, 1965; Chappell, 1969b; Pennycuick, 1971b; Gilbertson, 1980), but, vary with host age and size (Clarke, 1954; Freeman, 1965; Arme and Owen, 1967; Chappell, 1969b; Lester, 1969; Pennycuick, 1971b; Coad, 1972; Gilbertson, 1980; Reimchen, 1982).

Distributions of *Schistocephalus* in three-spined sticklebacks are overdispersed (Pennycuick, 1971c). The plerocercoids exhibit extensive somatic growth in this host, and in areas where infection levels are high, plerocercoids frequently comprise between 20 and 40% of the total host-parasite mass (Arme and Owen, 1967; Pennycuick, 1971b; Peacock, 1979). Occasionally, the weight of the parasite burden may exceed that of the host (Arme and Owen, 1967; Pennycuick, 1971b). Experimental evidence (Meakins and Walkey, 1973) and field data (Vik, 1954; Orr and Hopkins, 1969; Lester, 1969) indicate that plerocercoid growth is density-dependent. The *in*

vitro growth of plerocercoids of *Schistocephalus* is described by McCaig and Hopkins (1965) and Sinha and Hopkins (1967), and details of the *in vivo* growth of plerocercoids transplanted from one three-spined stickleback to another are given by Bråten (1966) and Meakins and Walkey (1973), however, there is little information available regarding the growth of the parasite in the field.

Recruitment takes place primarily in the spring and summer months (Hopkins and Smyth, 1951; Clarke, 1954; Pennycuick, 1971a; Meakins and Walkey, 1973). Pennycuick (1971a) reports that some new invasions occurred during the winter months in a population of sticklebacks in England, however, this is unlikely to occur in regions which experience much colder winters (Chubb, 1980).

In this chapter, the infection dynamics of *S. solidus* in *G. aculeatus* at Matamek Lake are described. One of the specific aims of this investigation was to follow the progress of the infection in relation to the life history of the host. Consequently, it will be seen that the infection variables have been determined separately for different age classes of sticklebacks. The aquisition and subsequent growth of a cohort of plerocercoids are monitored, and multiple infections are examined to obtain an estimate of plerocercoid growth and longevity in the field.

The infection dynamics of *Schistocephalus* in *Gasterosteus* at Matamek Lake are compared with those previously described for populations from other locations, and discussed in relation to both field and laboratory studies.

RESULTS

Seasonal variations in the parasite prevalence, mean intensity ($\bar{x}$), abundance and mean Parasite Index (P.I.) of sticklebacks collected at Matamek Lake from July 1981 to June 1983 are presented in Figures 9 to 12. (The data are tabulated in Tables i and ii of the Appendix.)

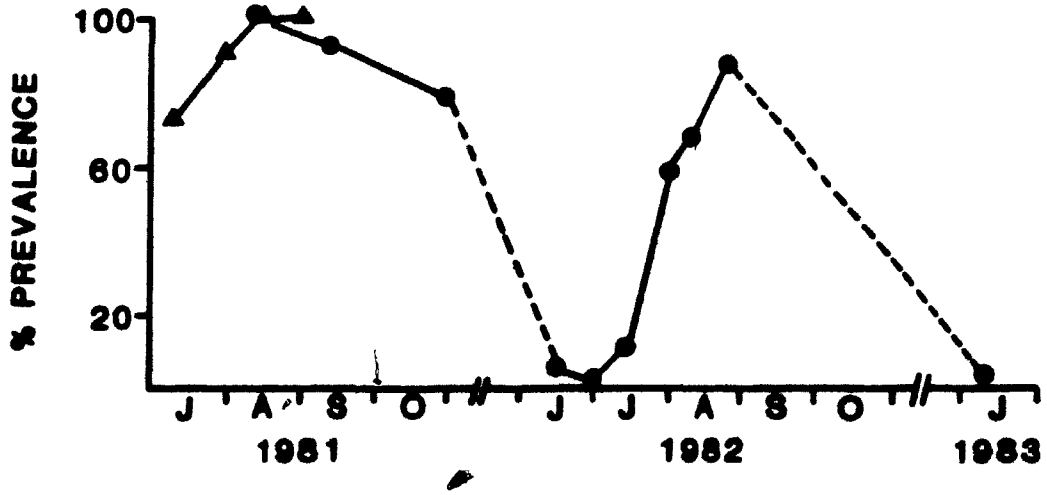
Figures 9A to 12A show the values of these variables for all sticklebacks collected on each sampling date, irrespective of the age of the fish. Henceforth in the text these samples of fish are referred to as the "complete" samples. Data from both sample sites are presented. In Figures 9B to 12B, seasonal variations in prevalence, mean intensity, abundance and mean P.I. for specific age classes of fish are given, with the data from the South camp excluded, because it was not possible to determine the ages of fish from that location.

Prevalence values for the complete samples were below 10% at the onset of sampling in June 1982 and June 1983. Prevalence increased throughout the summer, reaching values of 99% and 89% in August 1981 and August 1982 respectively, and then dropped slightly in September and October (Figure 9A). These high prevalence values reflect the age composition of the samples. In August, September and October, 1+ fish predominated; virtually all these fish were infected (Figure 9B). The drop in prevalence for complete samples in September and October resulted from the inclusion of uninfected young of the year (0+). Mean intensity and P.I. values for complete samples also increased as the summer progressed, reaching

Figure 9. Seasonal prevalence values for sticklebacks infected with S. solidus, 1981 - 1983.

A. Prevalence values for all sticklebacks collected on each sampling date, irrespective of the age of the fish. ▲ - South camp. ● - North camp.

B. Prevalence values for specific cohorts of fish. ■ - 1+ (1981). ● - 0+ (1981), 1+ (1982), 2+ (1983). ○ - 3++ (1982). □ - 0+ (1982), 1+ (1983). △ - 3++ (1983).


100
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% PREVALENCE
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1981
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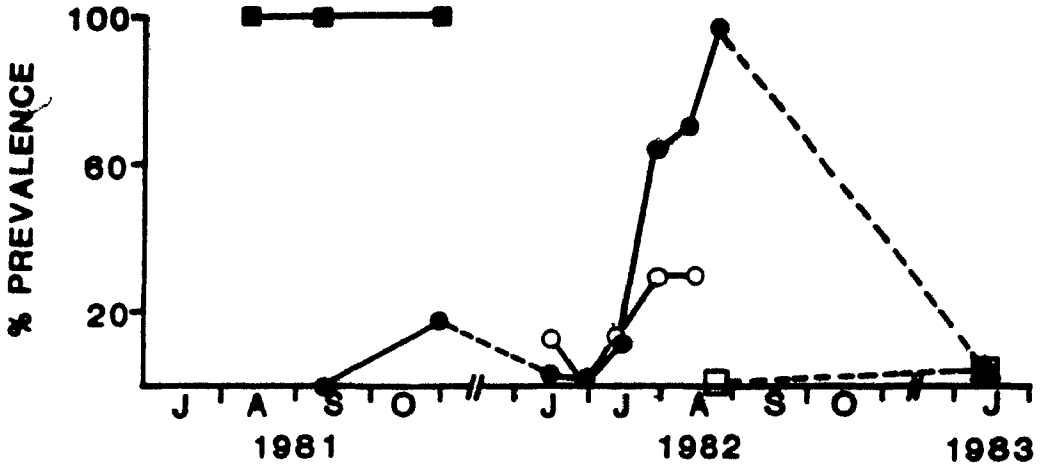
100
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1981
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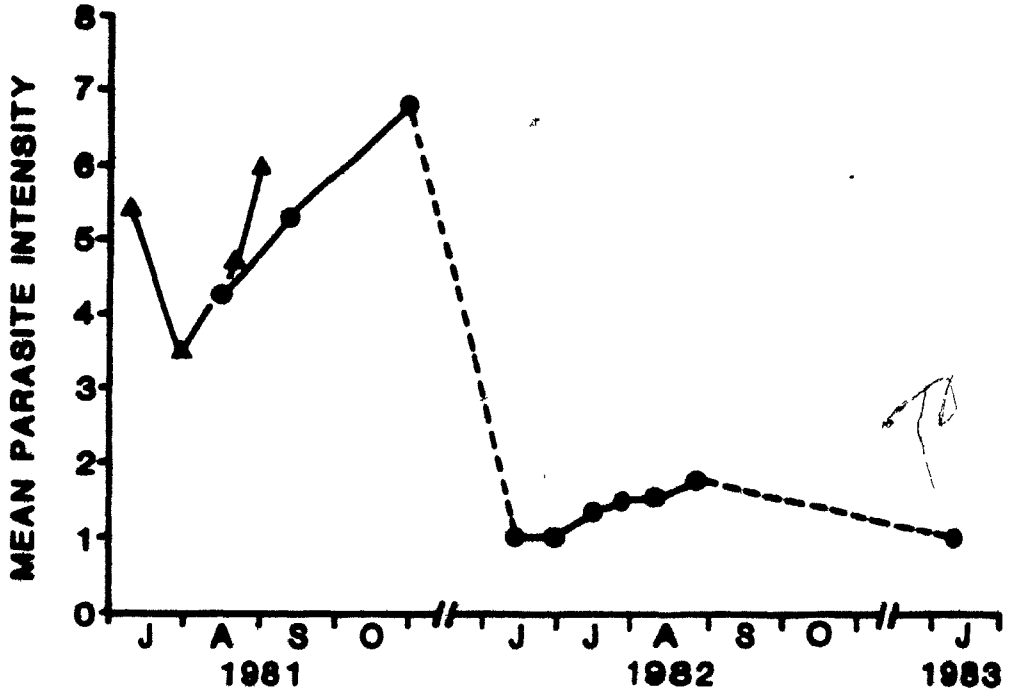
1983

B

Figure 10. Seasonal mean parasite intensities for three-spined sticklebacks infected with S. solidus.

A. Mean parasite intensities for all infected sticklebacks collected on each sample date, irrespective of the age of the fish. ▲ - South camp. ● - North camp.

B. Mean parasite intensities for specific cohorts of fish. ■ - 1+ (1981). ● - 0+ (1981), 1+ (1982), 2+ (1983). ○ - 3++ (1982). □ - 1+ (1983). △ - 3++ (1983).


MEAN PARASITE INTENSITY
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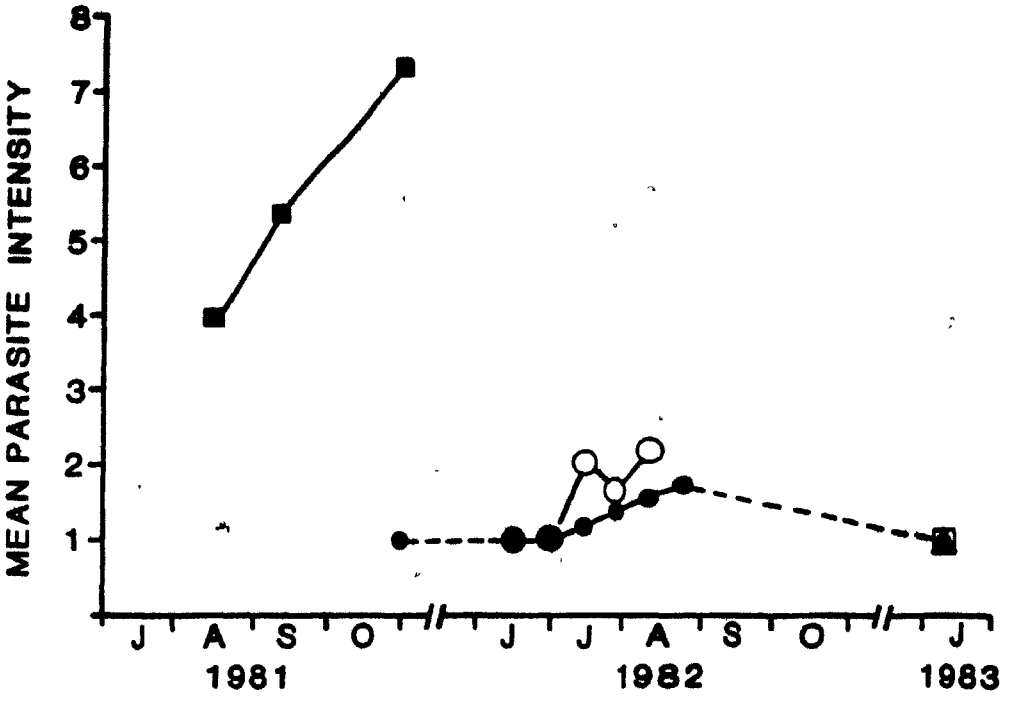
MEAN PARASITE INTENSITY
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J
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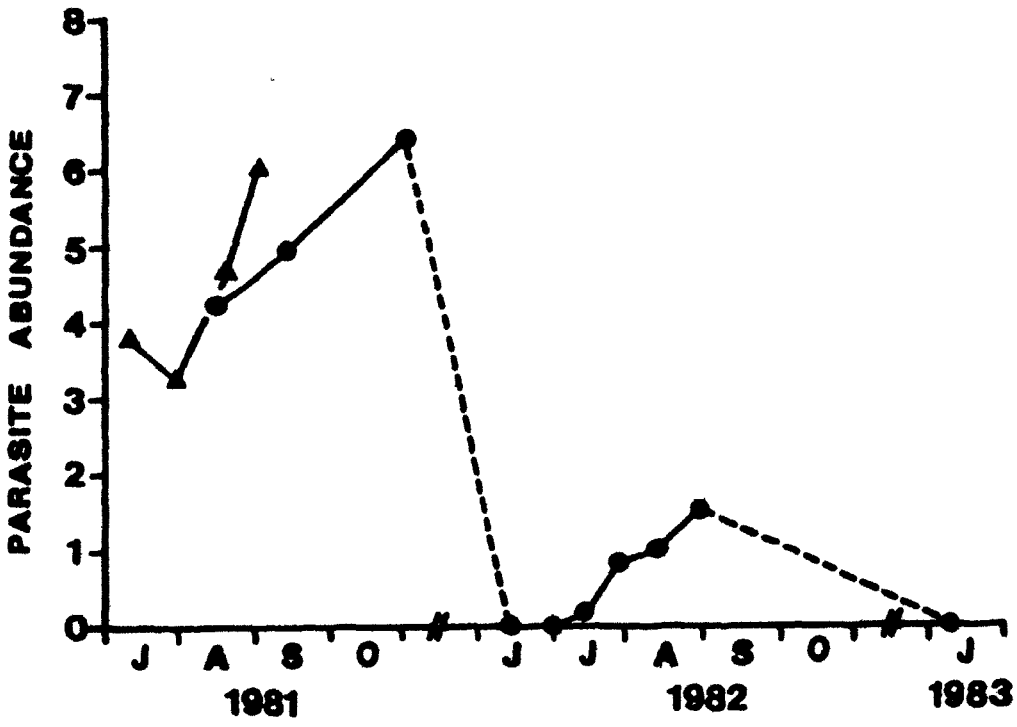
O
J
1981
1982
1983

B

Figure 11. Seasonal changes in the abundance of plerocercoids of S. solidus.

A. Abundance of S. solidus in all sticklebacks collected on each sample date, irrespective of the age of the fish. ▲ - South camp. ● - North camp.

B. Abundance of S. solidus in specific cohorts of sticklebacks. ■ - 1+ (1981). ● - 0+ (1981), 1+ (1982), 2+ (1983). ○ - 3++ (1982). □ - 1+ (1983). △ - 3++ (1983).


PARASITE ABUNDANCE
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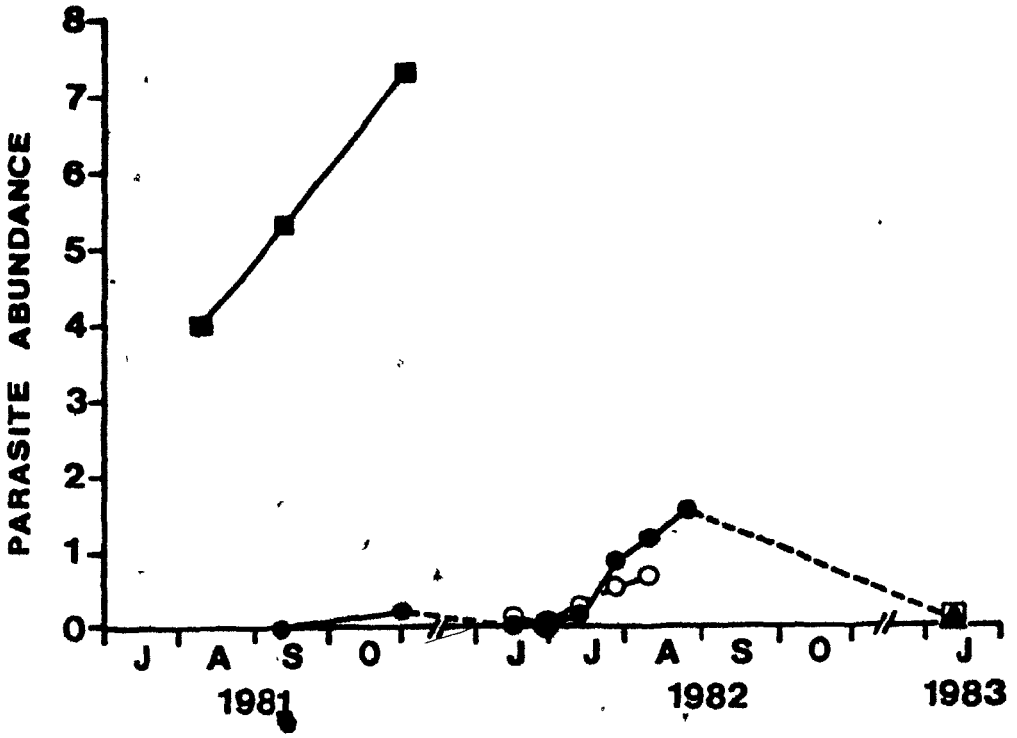
PARASITE ABUNDANCE
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1983
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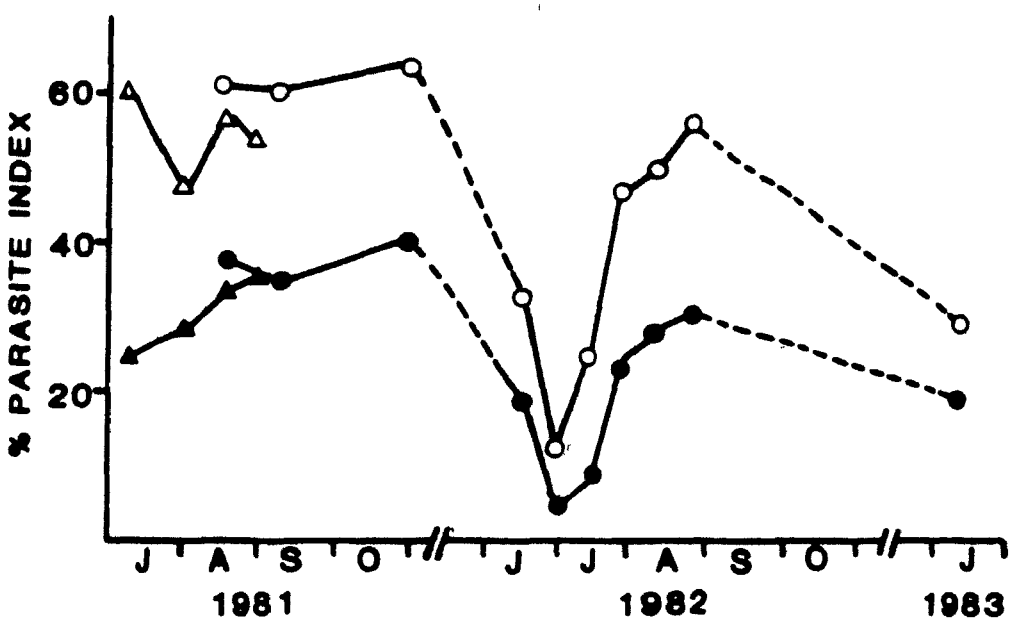
Figure 12. Seasonal changes in the Parasite Index of G. aculeatus infected with S. solidus.

A. Mean (shaded) and maximum (unshaded) Parasite Indices of all infected sticklebacks collected on each sampling date, irrespective of the age of the fish. ▲, △ - South camp. ●, ○ - North camp.

B. Mean Parasite Indices of specific cohorts of fish. ■ - 1+ (1981). ● - 0+ (1981), 1+ (1982), 2+ (1983). ○ - 3++ (1982). △ - 3++ (1983).


% PARASITE INDEX
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S
O
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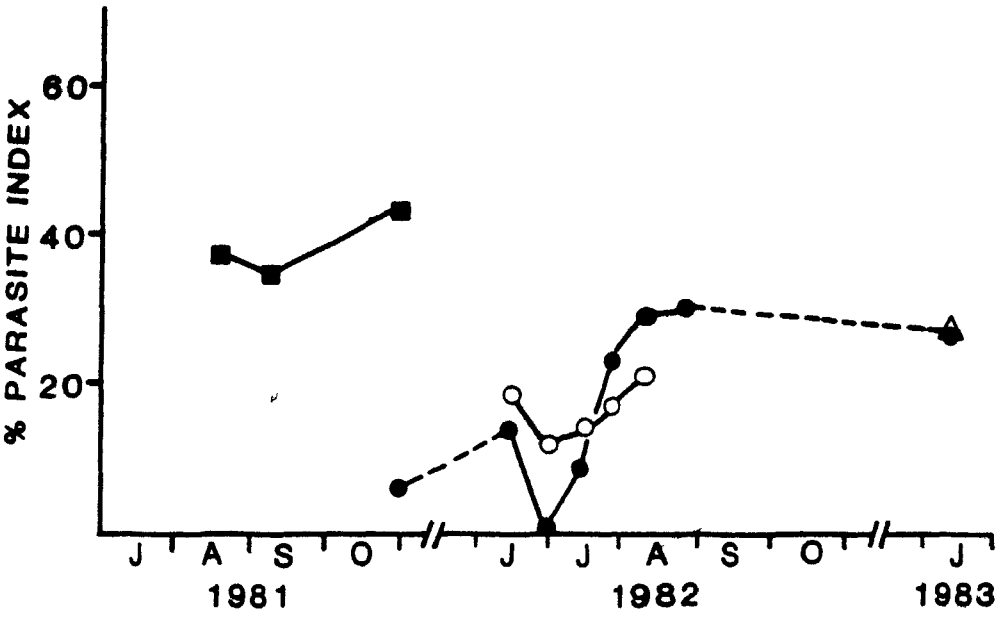
J
A
S
O
J
1981
1982
1983

A


% PARASITE INDEX
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1981
1982
1983

B

maximum values in October, at the end of the sampling period (Figures 10A and 12A). Seasonal variations in the prevalence and mean P.I. did not differ greatly from year to year (Figures 9A and 12A), however, there was a marked difference in the mean intensities of complete samples of sticklebacks collected in 1981 and 1982: in August 1981, $\bar{x}=4.3$, range (1-24); in August 1982, $\bar{x}=1.7$, range (1-7) (Figure 10A).

From August to October the average P.I. varied from 30 to 40% (Figure 11A). Maximum P.I. values greater than 50% were recorded from July through October in 1981 and in August 1982, indicating that some sticklebacks carry a parasite burden which exceeds their own body weight.

It is possible to follow the changes in prevalence of a cohort of fish during the first two years of life (Figure 9B). The young of the year were uninfected in September 1981, but by late October 1981 18% of them were infected. The prevalence dropped to 3.2% in June 1982, started to rise again in early July, showed a maximum rate of increase in late July and by August prevalence approached 100%. Although no more samples were collected in 1982, the trend in 1981 suggests that the prevalence would have remained high in this age class for the remainder of the sampling season. The 2+ year class was poorly represented in June 1982 and 1983, but the available evidence indicates that the prevalence dropped dramatically over the second winter of life (1982/83) to a value of less than 10% in June.

The 2+ year class was absent at all other times during the sampling period; thus, comparisons between the infection

characteristics of different age classes are largely restricted to the 0+, 1+ and 3++ year groups. Prevalence values of the cohort of fish designated as 3++ were marginally higher than those of their 1+ counterparts in June and early July 1982, but for the rest of the season prevalence in this age group was lower than that observed in 1+ fish. Mean intensities of both 1+ and 3++ fish were similar in 1982 (Figure 10B), and the mean P.I. values of the two age classes followed a similar pattern to the prevalence (Figure 12B).

Seasonal data on prevalence and mean intensity are summarized in Figures 11A and 11B which show the changes in relative density or abundance (prevalence x mean intensity) of plerocercoids of Schistocephalus over the sampling period for complete samples and specific age classes of fish respectively. Abundance was at a minimum in June, however it increased from August through October in 1981 and during July and August 1982, indicating that sticklebacks may become infected or reinfected at any time from July to late October. At the North camp, the maximum rate of increase in abundance of parasites occurred in late July 1982. A relatively greater increase in the abundance of plerocercoids of S. solidus was observed in August 1981 at the South camp, however, these data should be viewed with caution because mixed sampling methods were employed at this location. The abundance of parasites in complete samples of sticklebacks dropped one hundredfold between October 1981 and June 1982.

Seasonal changes in the distribution of Schistocephalus in complete samples of Gasterosteus collected between August

1981 and August 1982 at the North camp are shown in Figure 13. The increase in the number of uninfected fish in September and October again reflects the recruitment of fry into the fish population. Although the majority of sticklebacks in 1981 had 5 plerocercoids or less, several fish harboured greater numbers of parasites, a few having more than 20 plerocercoids. One fish measuring 49mm collected in September 1981 was found to harbour 40 parasites. Between October 1981 and June 1982 the shape of the distribution changed dramatically; by June 1982, 94% of the fish sampled were uninfected (as compared to 20% in October 1981), with the infected fish carrying only one plerocercoid each. By mid July the majority of fish were still uninfected and the maximum number of plerocercoids found in a single host was 3. In early August nearly 70% of the fish were infected and by late August almost 90% of the fish were infected, and up to 8 plerocercoids were found in a single host. When the distributions for August 1981 and 1982 are compared, the differences in the level of infection between the two years are readily apparent.

Since plerocercoid weights may vary by two orders of magnitude within a given host, it is considered that Parasite Indices, rather than numbers of plerocercoids, give a better indication of the level of infection in the host population (Arme and Owen, 1967). Seasonal changes in the frequency distributions of Parasite Indices of all infected fish are given in Figure 14, with the frequency distributions of specific age classes superimposed on the original histograms constructed for complete samples. Within each sample and within each age class

Figure 13. Seasonal changes in the distribution of plerocercoids of S. solidus in G. aculeatus.

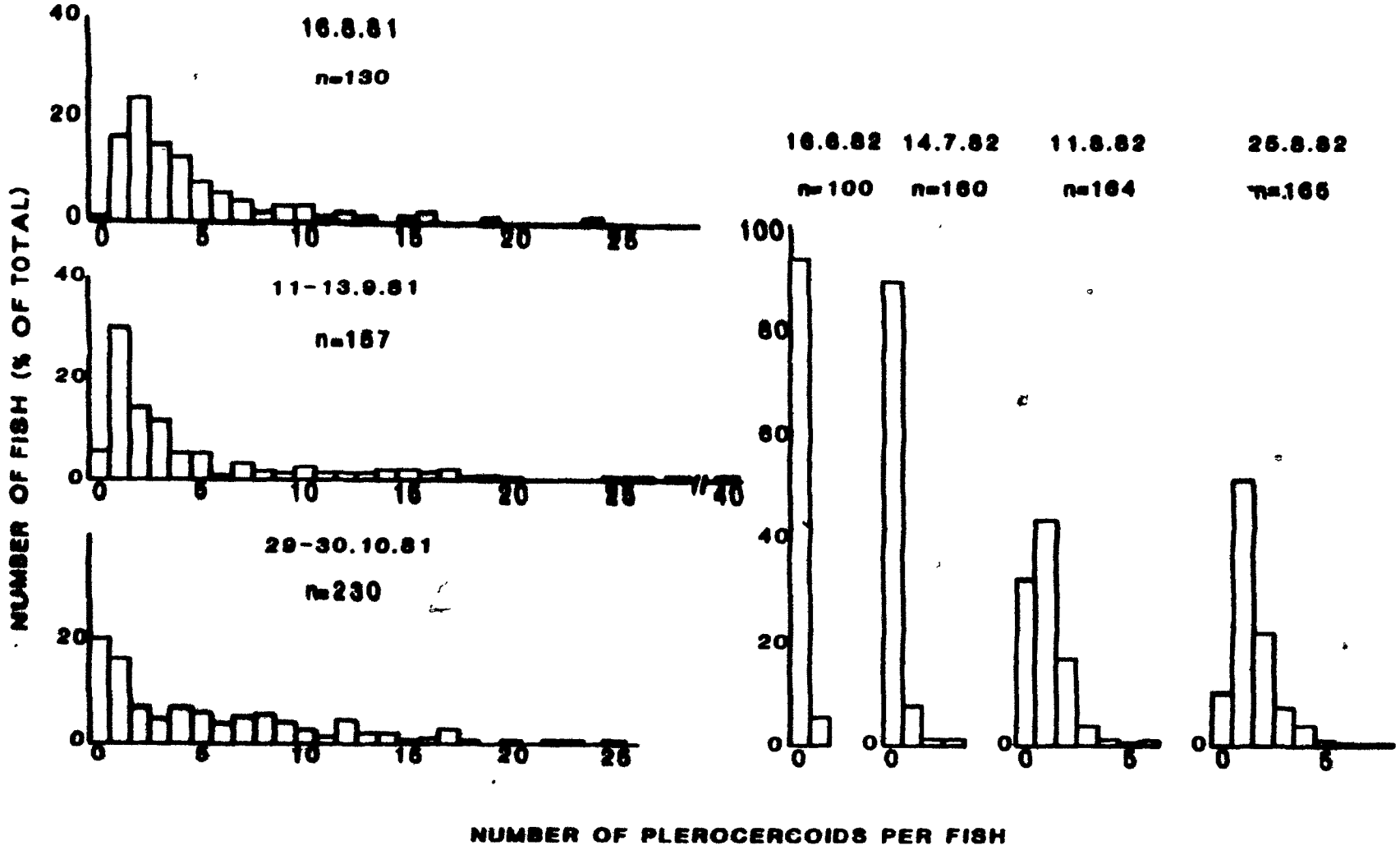
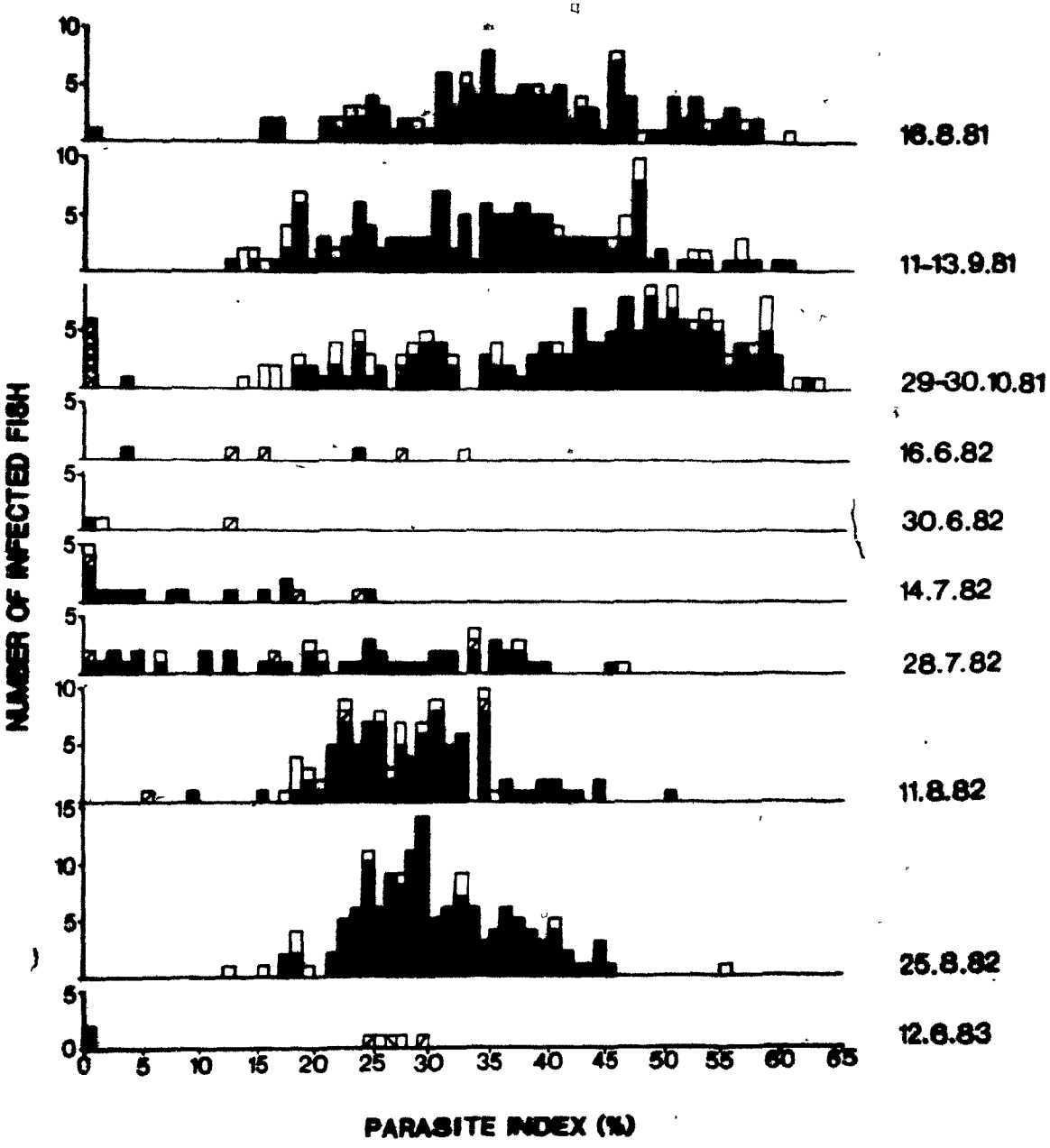

16.8.81
n=130
11-13.9.81
n=187
29-30.10.81
n=230
16.8.82
n=100
14.7.82
n=160
11.8.82
n=164
25.8.82
n=165
NUMBER OF FISH (% OF TOTAL)
NUMBER OF PLEROCERCOIDS PER FISH

Figure 14. Seasonal changes in the frequency distributions of Parasite Indices of infected sticklebacks collected at the North camp, 1981-1983. Stickleback ages are indicated by shading. □ - age unknown. ■ - 0+. ■ - 1+. ▧ - 2+. ▨ - 3++.


NUMBER OF INFECTED FISH
PARASITE INDEX (%)
16.8.81
11-13.9.81
29-30.10.81
16.6.82
30.6.82
14.7.82
28.7.82
11.8.82
25.8.82
12.6.83

the Parasite Indices cover a wide range of values. It seems likely that the observed differences in P.I. between 1+ and 3++ fish (see Figure 12B) reflect differences in the sample sizes rather than actual differences, since the ranges of the P.I. values are similar for the two age groups when they coexist. Parasite Indices of less than 10% are relatively uncommon in all samples except those collected in July. These low values are indicative of previously uninfected fish having become infected with small plerocercoids. The disappearance of heavily infected sticklebacks between October and June is particularly evident from this figure.

A comparison of the frequency distributions of the weights of plerocercoids from infections of different intensities (Figure 15) indicates that plerocercoid weight is inversely related to the intensity of the infection. Consequently, only data from single infections were used to examine plerocercoid aquisition and growth because the mean parasite intensity varied between samples. Since single infections were relatively uncommon in many samples, all available data from both sample sites was used to examine the seasonal changes in the weights of plerocercoids from single infections. The data are presented as a composite seasonal series of plerocercoid weight frequency distributions (Figure 16). Plerocercoids weighing less than 20mg dry weight were found predominantly in July and it was possible to follow the growth of this cohort of July recruits until the end of the season. A similar series of histograms, in which only the plerocercoids from single infections of hosts of known age are

Figure 15. Frequency distributions of the weights of plerocercoids of S. solidus from infections of different intensities. Only data on plerocercoids from 1+ sticklebacks collected in September is presented.

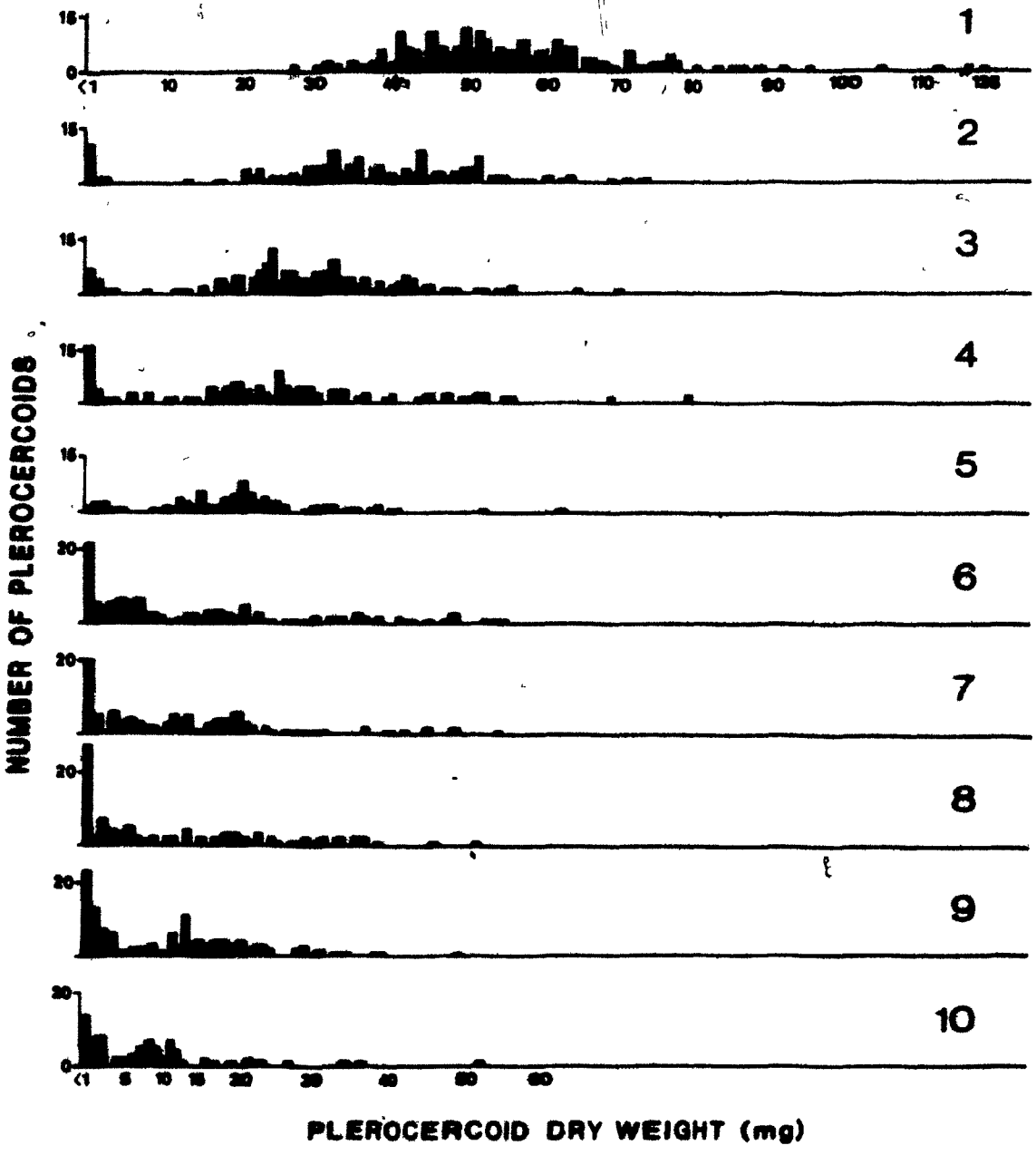
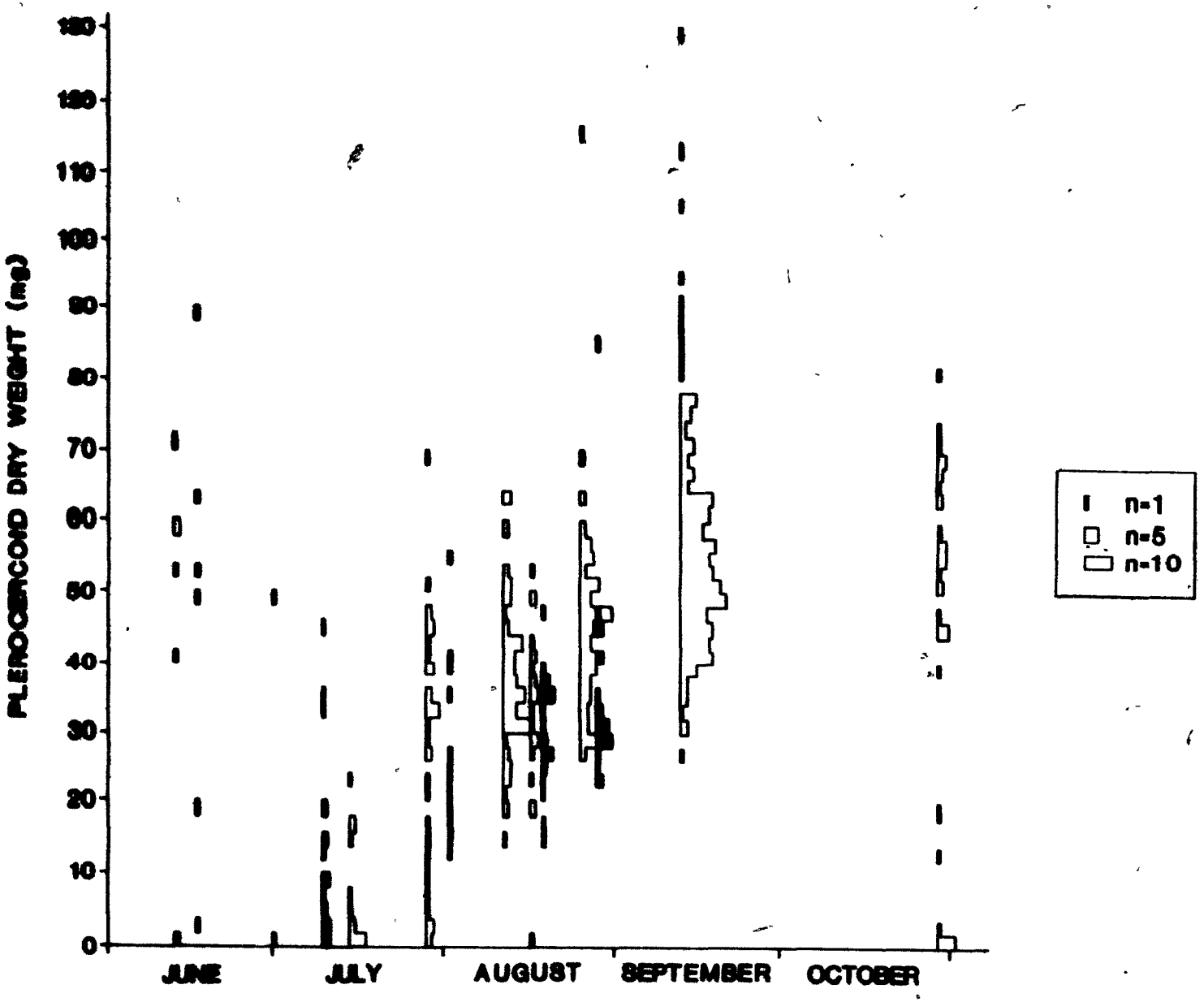

NUMBER OF PLEROCERCOIDS
PLEROCERCOID DRY WEIGHT (mg)
1
2
3
4
5
6
7
8
9
10

Figure 16. Seasonal weight frequency distributions for plerocercoids of S. solidus from all single infections. Data from the South camp are differentiated by shading. All other data come from collections made at the North camp. Overlap between adjacent distributions is shown by cross-hatching.


PLEROCERCOID DRY WEIGHT (mg)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
n=1
n=5
n=10

included, is given in Figure 17. Although the majority of small plerocercoids seen in July were found in 1+ fish, a few 3++ fish also acquired the infection. Since prevalence approached 100% in 1+ fish by late August, recruitment in September and October would necessarily have resulted in multiple infections and is only apparent in the young of the year. With the exception of a few very small worms (<4mg dry weight), which were probably early recruits, most of the single plerocercoids found in June weighed over 40mg (dry weight) and came from 2+ or 3++ fish. It is probable that these worms were at least a year old.

A composite growth curve for single plerocercoids in 1+ fish over one season is presented in Figure 18. It can be seen that single plerocercoids acquired in the early summer attained a mean dry weight of approximately 57 mg by the end of October.

As previously mentioned, plerocercoid weight was observed to be inversely related to parasite intensity (see Figure 15). The relationship between mean plerocercoid dry weight and parasite intensity, for 1+ fish collected in September 1981, is given in Figure 19. This particular sample of fish was selected to examine this phenomenon because the level of infection was high at this time (prevalence=100%, $\bar{x}$=5.3 (1-40) and mean P.I.=35%) and because this sample contained more fish than any other. The mean plerocercoid dry weight decreases with increasing parasite intensity, the mean weight of worms from fish having ten or more worms being less than one fifth of the weight of plerocercoids from single infections. The mean weight of the largest plerocercoid per fish also decreases with increasing parasite intensity (see Figure 20).

Figure 17. Seasonal weight frequency distributions for plerocercoids from sticklebacks with single infections collected at the North camp. The age of the host is indicated by the shading. ▨ - 0+. □ - 1+. ▧ - 2+. ■ - 3++.

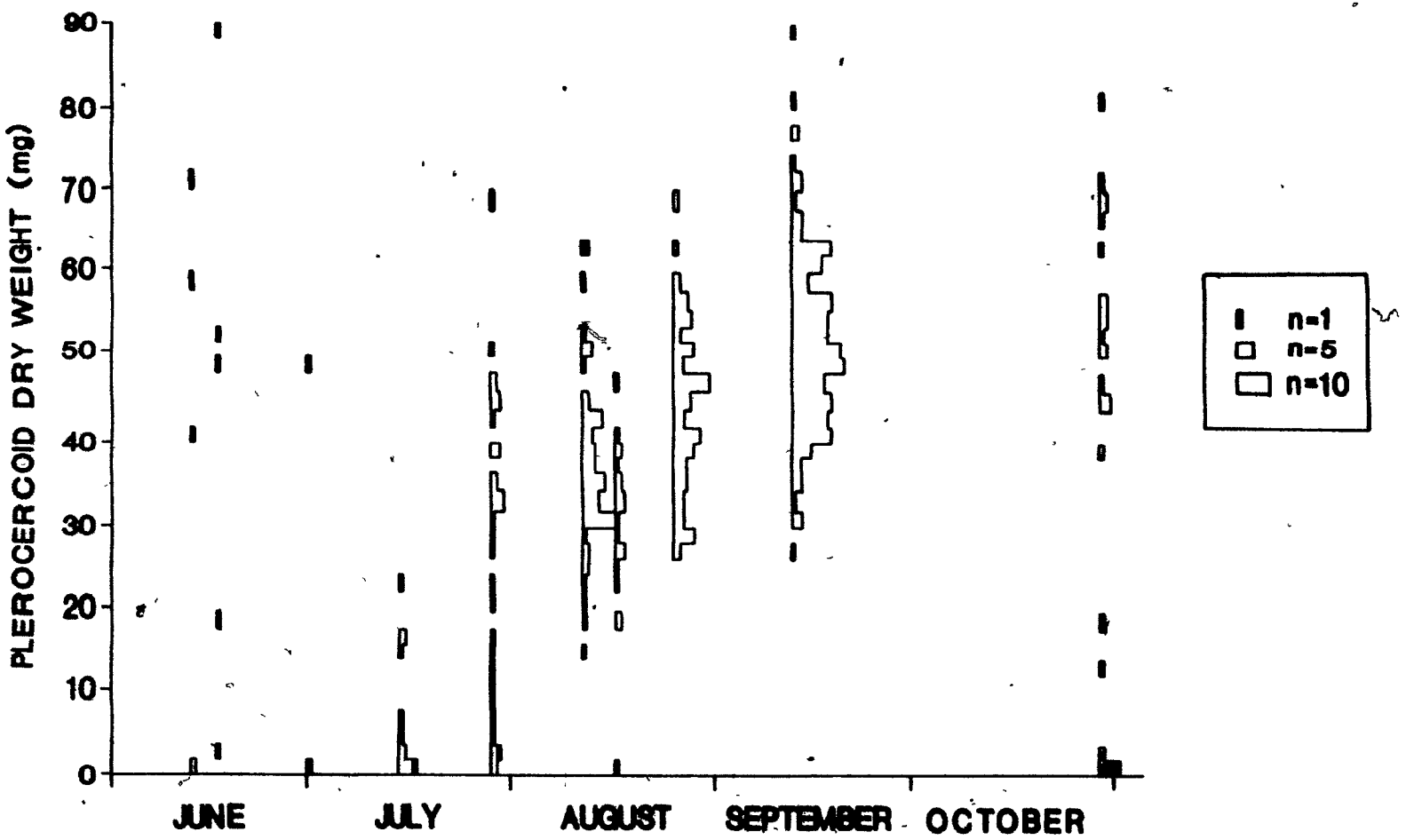

PLEROCERCOID DRY WEIGHT (mg)
90
80
70
60
50
40
30
20
10
0
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
n=1
n=5
n=10

Figure 18. Growth curve for plerocercoids of S. solidus from single infections of 1+ sticklebacks collected in 1981 and 1982 at the North camp. ○ - 1981. ● - 1982.

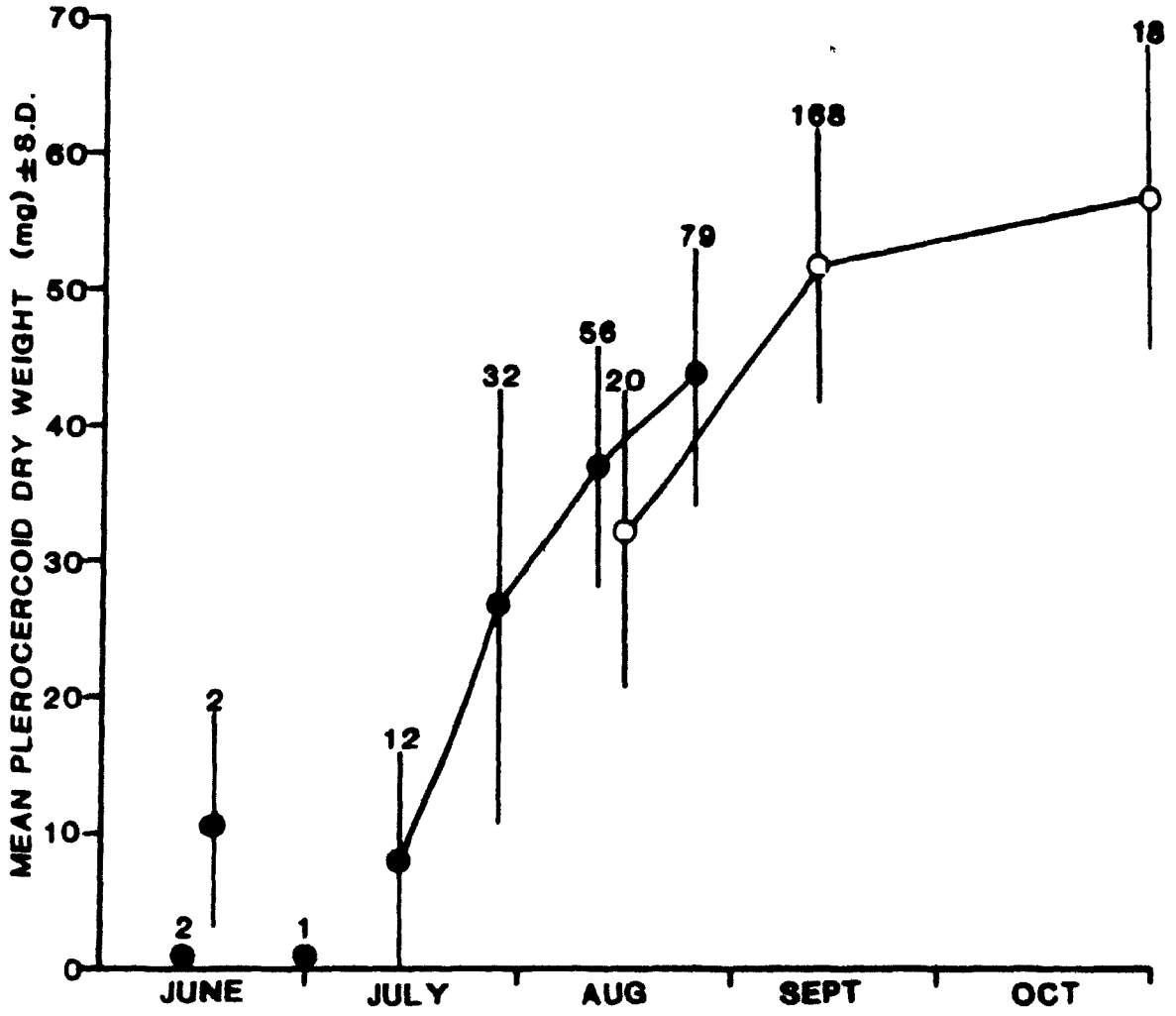

MEAN PLEROCERCOID DRY WEIGHT (mg) ± S.D.
70
60
50
40
30
20
10
0
JUNE
JULY
AUG
SEPT
OCT
2
2
1
12
32
56
20
79
168
18

Figure 19. Relationship between mean plerocercoid weight and parasite intensity for plerocercoids of S. solidus from 1+ sticklebacks collected in September 1981. Sample sizes are given below each point on the plot.

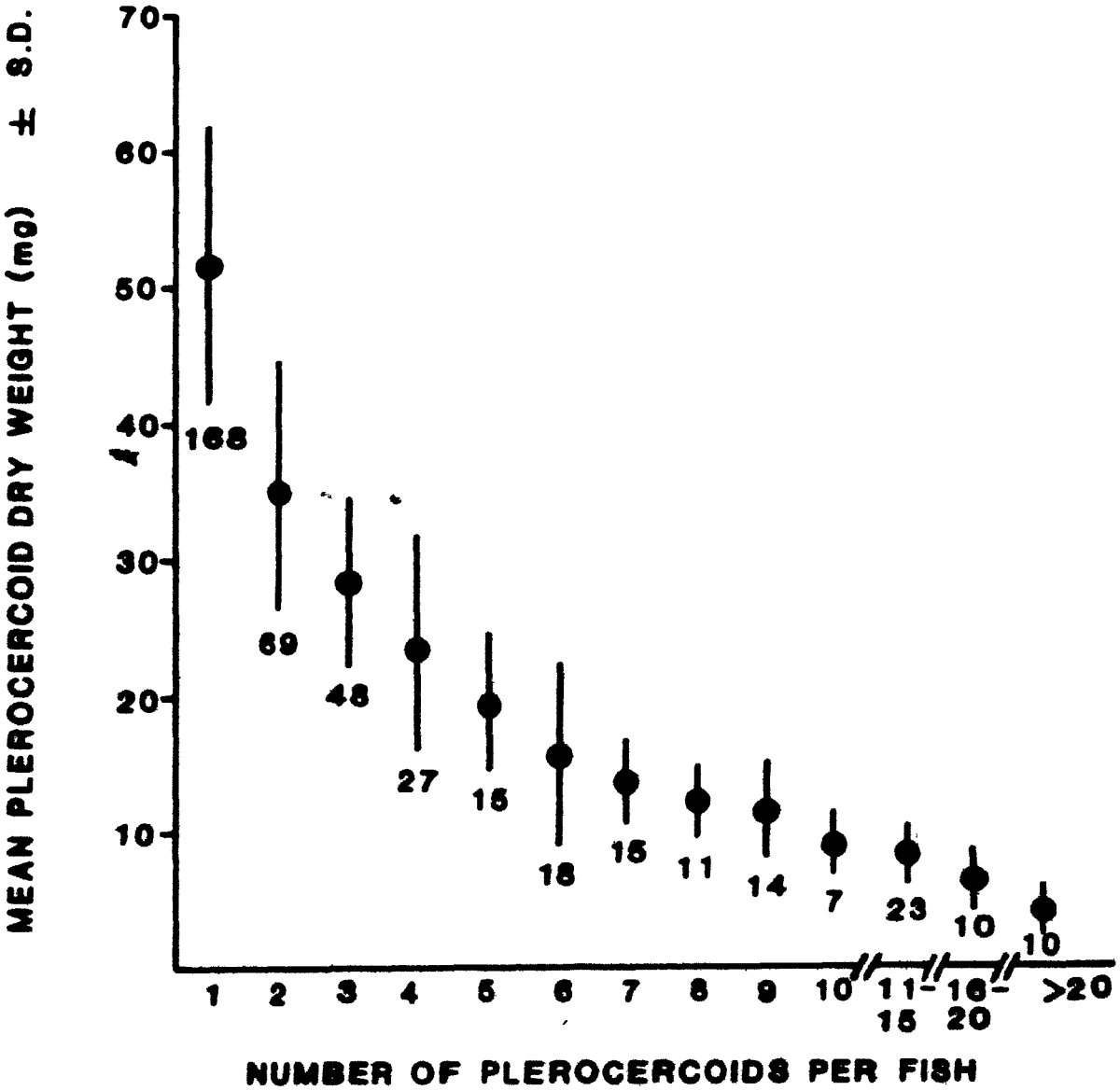
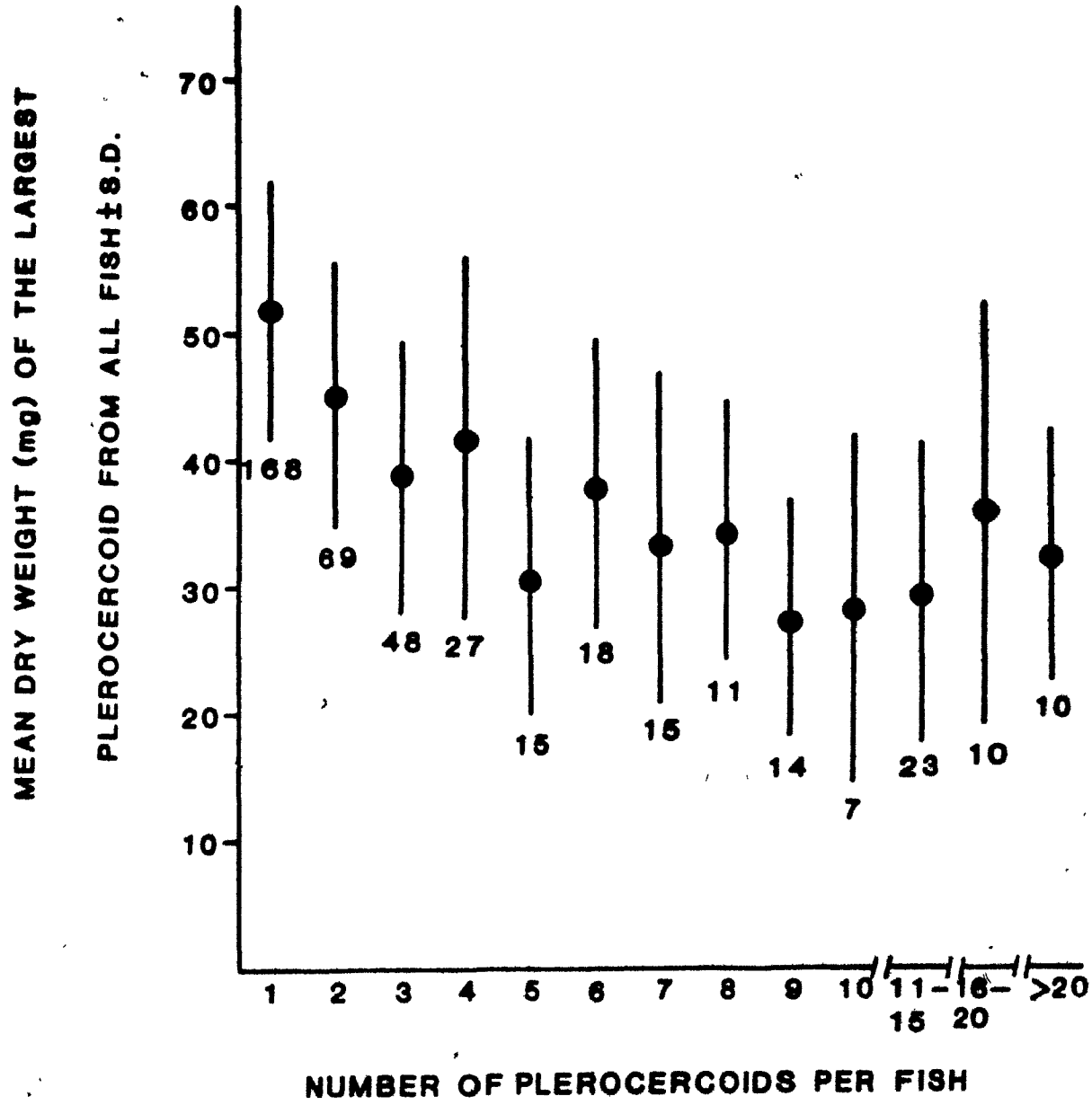

MEAN PLEROCERCOID DRY WEIGHT (mg) ± S.D.
70
60
50
40
30
20
10
168
69
48
27
15
18
15
11
14
7
23
10
10
1
2
3
4
5
6
7
8
9
10
11-15
16-20
>20
NUMBER OF PLEROCERCOIDS PER FISH

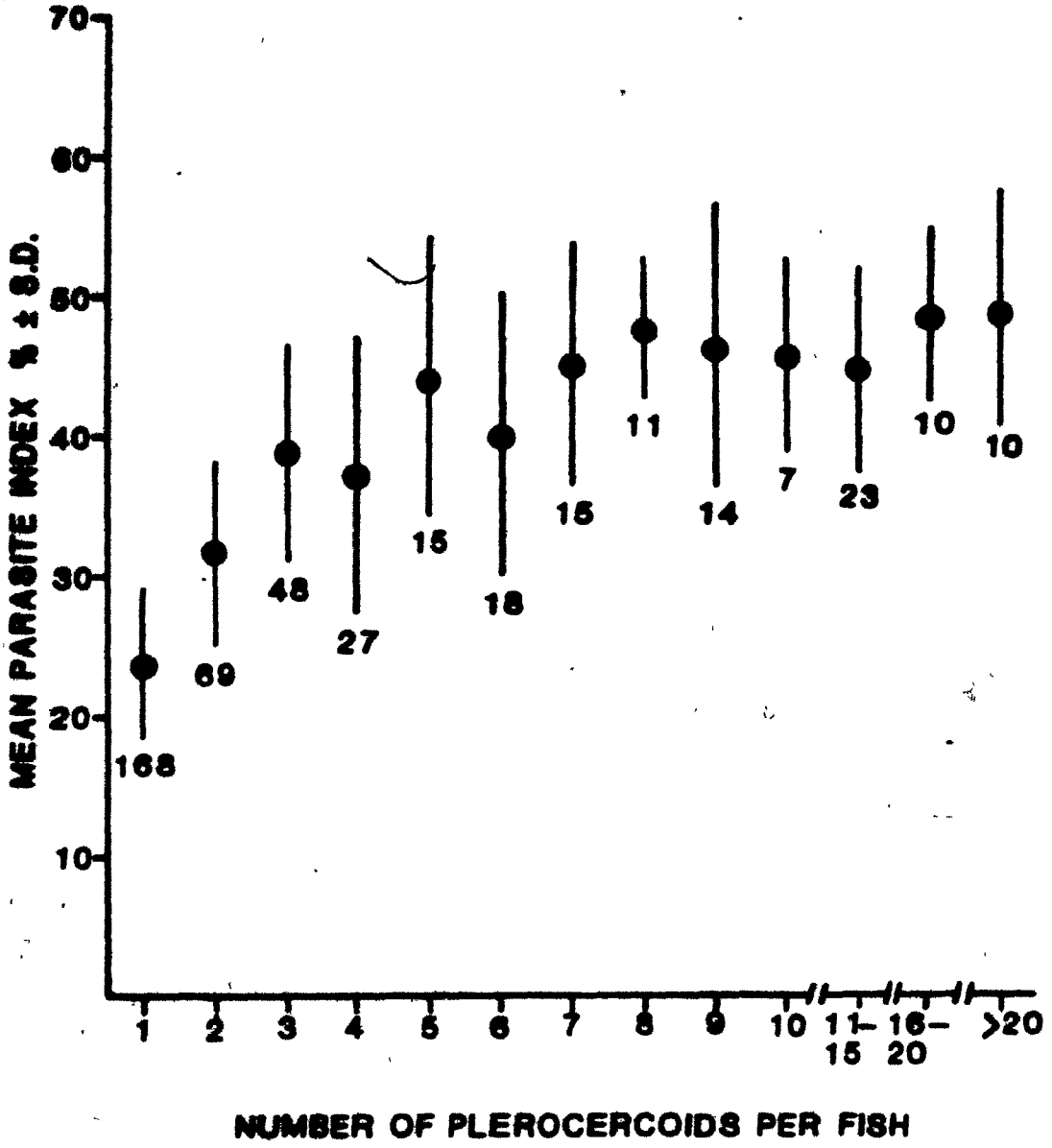
Figure 20. Relationship between the mean weight of the largest plerocercoid of S. solidus per fish and the parasite intensity for 1+ sticklebacks collected in September 1981. Sample sizes are given below each point in the plot.


MEAN DRY WEIGHT (mg) OF THE LARGEST PLEROCERCOID FROM ALL FISH ± S.D.
70
60
50
40
30
20
10
168
69
48
27
15
18
15
11
14
7
23
10
10
1
2
3
4
5
6
7
8
9
10
11–15
16–20
>20
NUMBER OF PLEROCERCOIDS PER FISH

The relationship between the mean Parasite Index and parasite intensity is also of interest (see Figure 21). At low parasite intensities the P.I. increases with increasing parasite intensity, but at higher intensities it reaches a plateau, at approximately 45%.

Since seasonal variations in abundance indicate that some recruitment may occur in September, then it follows that some of the small plerocercoids found in fish collected in September were new recruits. From the examination of the weights of plerocercoids from double infections (see Table iii in the Appendix) a pattern emerged: either (A) a small plerocercoid was found with a large plerocercoid (the latter being comparable in size to plerocercoids found in single infections); or (B) both plerocercoids were of similar size being smaller than the large plerocercoids from type "A" infections. Type "A" infections accounted for 19% of the double infections examined. It is probable that the small plerocercoids in type "A" infections were new recruits. From Figure 15 it may be seen that for parasite intensities of 2 to 5, plerocercoids of 4mg dry weight or less appear to form a fairly discrete cohort set apart from the rest of the plerocercoids. On the assumption that these small parasites are new recruits and that all plerocercoids of comparable size are also new recruits, regardless of the intensity of infection, all fish bearing plerocercoids of 4.5mg dry weight or less were omitted and the relationships between mean plerocercoid weight, mean weight of the largest plerocercoid and P.I. and parasite intensity were then re-examined. In addition, the same relationships were examined for

Figure 21. Relationship between mean Parasite Index and the parasite intensity for 1+ sticklebacks collected in September 1981. Sample sizes are given below each point in the plot.


MEAN PARASITE INDEX % ± S.D.
70
60
50
40
30
20
10
168
69
48
27
15
18
15
11
14
7
23
10
10
1
2
3
4
5
6
7
8
9
10
11–15
16–20
>20
NUMBER OF PLEROCERCOIDS PER FISH

sticklebacks collected in October. The data are shown in Figures iiiA-F in the Appendix. (The relationship between plerocercoid dry weight and parasite intensity for 1+ sticklebacks collected in October 1981 (Figure iv in the appendix) is given, to show that the removal of all plerocercoids measuring <4.5mg is also juqifiable for the October sample.) Although the sample sizes are considerably smaller the same patterns are apparent. Thus it is assumed that the relationships between mean plerocercoid weight, weight of the largest plerocercoid and mean P.I. and parasite intensity, given in Figures 19-21 are not unduly affected by the presence of new recruits.

DISCUSSION

At Matamek Lake the number of infected fish was low (prevalence <10%) at the beginning of the sampling season in June of both years. At the end of the sampling season in October 1981, nearly all fish were infected. Similar increases in prevalence over the summer months have been reported for all populations of Schistocephalus in Gasterosteus studied seasonally in North America to date, although maximum prevalence levels vary between these populations, ranging from 50 to almost 100% (Freeman, 1965; MacLean, 1974; Peacock, 1979; Gilbertson, 1980; Reimchen, 1982). In the present study the overall Parasite Index (P.I.) also increased from spring through autumn to approach a mean value of 41% in October. Peacock (1979) noted that the mean P.I. of infected fish from British Columbia

rose significantly throughout the growing season to reach a value of 25% in September.

Chappell (1969a), Pennycuick (1971a), and Arme and Owen (1967) describe the seasonality of populations of sticklebacks infected with Schistocephalus in the U.K.. Chappell (1969a) found prevalence to be highest (55%) in a May/June combined sample, and the mean parasite intensity also reached a maximum ($\bar{x}$=1.6 range=1-4) at this time of year. Pennycuick (1971a) noted an increase in the prevalence, mean intensity and P.I. from June (prevalence=72%, $\bar{x}$=1.4 and P.I.=20%) through October (prevalence=98%, $\bar{x}$=8.5 and P.I.=35%). Arme and Owen (1967) combined their data into quarterly means, making the trends a little less discernible, however, prevalence was highest (96%) in April-June and July-September in 1963 and the mean parasite intensity was at a maximum ($\bar{x}$=12.3) in April-June of the same year.

The infection is not evenly distributed between host age classes. Prevalence levels in 1+ fish at Matamek Lake were found to be considerably higher than in 0+ and 3++ fish. Maximum prevalence values were 100%, 18% and 30% respectively. Infected fry were only found in October. The mean parasite intensity of 3++ fish was marginally higher than that of 1+ fish in 1982, the combined means for June, July and August of that year for the two age classes were 2.0 and 1.5 respectively. The mean parasite intensity in 1+ fish the previous year, however, reached a maximum of 7.3 in October. Young of the year never had more than one plerocercoid. Coad (1972), who also sampled sticklebacks at Matamek Lake in August 1970, reported prevalence

values and mean intensities of 0, 90 and 68%, and 0, 1.7 and 1.9 for his designated 0+, 1+ and 2+ age classes respectively; the mean intensities were comparable to those found at Matamek in August 1982. Freeman (1965) and Lester (1969) found that prevalence was highest in an intermediate size group of fish and Arme and Owen (1967) found that the mean P.I. and parasite intensity were inversely related to fish size (young of the year were not included in their samples). Pennycuick (1971b) also found that the prevalence, mean parasite intensity and mean P.I. were highest in 1+ fish, although 0+, 2+ and 3+ fish were all heavily infected. In all the aforementioned studies maximum prevalence levels were high, frequently approaching 100%. In contrast, in the populations described by Chappell (1969a,b), Gilbertson (1980) and Reimchen (1982) prevalence rarely exceeded 50% and prevalence increased with fish age.

In areas where infection levels are very high a few hosts may harbour large numbers of plerocercoids. Pennycuick (1971a), Hopkins and Smyth (1951), Arme and Owen (1967) and Smyth (1946) describe single hosts infected with as many as 106, 130, 138 and 140 plerocercoids respectively. In the present study the maximum number of plerocercoids found in one stickleback was 40.

In populations where multiple infections are common, the weight of a given stickleback may be exceeded by that of its parasite burden. Sticklebacks with a P.I. greater than 50% were found at Matamek Lake in August, September and October 1981, and in August 1982. One fish collected in October 1981 had a P.I. of 62%. Maximum P.I. values of 62% and 69% have been reported by Pennycuick (1971b) and Arme and Owen (1967) respectively.

In the present study the parasite abundance in 1+ fish and in complete samples of fish in August 1981 was more than double that of comparable fish collected in August 1982. Differences in infection levels from year to year are also described by Arme and Owen (1967) and Pennycuick (1971a). In the population examined by Arme and Owen (1967) the prevalence and mean intensity of Schistocephalus and the mean P.I. decreased from 100%, 46.5 and 47% respectively in 1962, to 59%, 10.5 and 40% respectively in 1963, to 36%, 1.3 and 15% respectively in 1964. Pennycuick (1971d) also noted annual variations in the relative strengths of stickleback age classes. Consequently she proposed a mechanism to account for a 4 or 5 year cyclical fluctuation in Gasterosteus and Schistocephalus populations. On the assumption that a heavy infection with plerocercoids of Schistocephalus makes hosts more susceptible to predation and to mortality due to other stresses, Pennycuick (1971d) suggests that the infection builds up in Gasterosteus aculeatus until many fish die, are eaten by predators or are prevented from breeding (see previous chapter). This causes a gradual decline in the numbers of fish in the population and hence the size of the parasite population. As the number of fish decreases and the infection becomes lighter, breeding becomes more successful, hosts are generally less vulnerable to predation and mortality due to other stresses, and the number of fish in the population increases. This in turn enables the S. solidus infection to build up once more. These fluctuations would be modified by other external factors, such as food supply, winter temperature and the abundance of other host

species in the life cycle (Pennycuick, 1971d).

Between October and April (1966/1967) and September and March (1967/1968), Pennycuick (1971d) collected 89 dead sticklebacks from the edge of Priddy Pool. The plerocercoids contained in these dead fish had a larger mean weight than those found in live fish, and the mean P.I. of the dead fish was 36% as compared to 27% for living fish. Pennycuick attributed the death of these fish to a combination of their high levels of parasitism, harsh winter conditions and scarcity of food.

There is much evidence to suggest that heavy burdens of Schistocephalus impose stress on their fish hosts and may contribute to host mortality. Lester (1971) reported that parasitized sticklebacks die sooner than uninfected fish when kept in aquaria, mortality rates rising when the parasitized fish were subjected to dietary and high temperature stresses. Pascoe and Mattey (1977) and Walkey and Meakins (1970), and Pascoe and Woodworth (1980) describe increased mortality in parasitized fish subjected to dietary stress and increased cadmium levels respectively. Threlfall (1968) attributed a mass die-off of three-spined sticklebacks to joint stress imposed by high levels of Schistocephalus solidus and the ectoparasite Argulus canadensis. Vik (1954) noted that the fat deposits commonly associated with the alimentary canal of sticklebacks were absent in parasitized sticklebacks. The role of Schistocephalus in retarding sexual maturation in female sticklebacks was discussed extensively in the previous chapter. These phenomena indicate that the plerocercoids compete with the host for energy resources, and in heavy infections the parasites

deplete host energy reserves and divert host energy from reproduction for their own use (Meakins, 1974b). The significant differences in the lengths and weights of infected and uninfected individuals (Pennycuick, 1971d; present study) suggest that infected fish are unable to meet the increased energy requirements imposed on them by their parasite burden. Consequently, when food is scarce it seems likely that selective mortality of heavily infected fish will occur because these fish are already suffering from some measure of starvation. Walkey and Meakins (1970) suggest that at a time when food supplies are low, so is the feeding rate of fish but so also should be the calorific demands made by the parasite upon its host. Consequently they state that decreases in the prevalence of infection resulting from the starvation of infected fish hosts are unlikely to occur. However, evidence presented by Spencer Davies and Walkey (1966) indicates that thermal acclimation occurs in plerocercoids, that is, their rate of metabolism at low temperatures is higher than expected, and Sinha and Hopkins (1967) report that plerocercoids will continue to grow *in vitro*, albeit to a limited extent, at temperatures as low as 4°C. Thus the energy demands made by the parasites during the winter may be higher with respect to host supply than in the summer. In the light of Pennycuick's (1971d) findings that the mean P.I. of dead fish collected over the winter was higher than that of living fish, it does seem highly probable that selective mortality of the most heavily infected fish does occur when food is scarce and worm burdens are high.

Such mortality may account for the decrease in infection

level with respect to host age observed in populations when infection levels are high (Pennycuick, 1971b, Arme and Owen, 1967; present study). Once acquired, plerocercoids are not lost from the abdominal cavity, thus, any drop in the infection level from one age class to the next must reflect selective mortality of infected fish.

In the present investigation, prevalence, mean intensity and mean P.I. values dropped dramatically over winter, suggesting that parasite-induced mortality may have occurred during this period. Since the prevalence of Schistocephalus was 100% and the mean P.I. was approximately 44% (higher than that reported for dead fish by Pennycuick (1971d)) in 1+ fish in October 1981, it is probable that parasite-induced mortality may have been partially responsible for the absence of 2+ fish in 1982. In addition, selective mortality of infected fry may have occurred since the prevalence in the young of the year also dropped between October 1981 and June 1982. (Plerocercoids of Triaenophorus nodulosus are reported to be responsible for the mortality of burbot fry (Lopukhina et al. 1973)). Thus, we may have witnessed a crash in both parasite and host populations, such as that proposed by Pennycuick (1971d). This would account for the lower mean parasite intensities observed in August 1982 as compared to August 1981. However, it is also possible that the samples collected were not representative of the total stickleback population in the lake, because spatial segregation of sticklebacks of different age classes is known to occur (Rogers, et al., 1967, cited by Manzer, 1976). Two year old fish may have been present outside the sampling area. Infection

levels in the 3++ class were lower than in the 1+ class, and this may provide indirect evidence for parasite-induced host mortality, but it should be noted that the infection level of the 3++ age class may have been underestimated, because the samples were collected from stickleback breeding grounds, and evidence suggests that infected sticklebacks are less likely to breed than uninfected fish (see previous chapter for details).

Thus, it is difficult to assess to what extent the observed seasonality of Schistocephalus in Gasterosteus, at Matamek Lake, is a product of parasite-induced host mortality, be it mediated indirectly by increasing the vulnerability of the host to predators, or directly by making excessive energy demands on the host, or seasonal changes in the relative distribution of infected and uninfected sticklebacks and fish of different age classes. Pope (1973) examined the stomach contents of brook trout (Salvelinus fontinalis, arctic char (Salvelinus alpinus) and rainbow smelt (Osmerus mordax) from Matamek Lake over the summer of 1970 and found that sticklebacks (three- and nine-spined) were of relatively little importance in the diet of these three potential fish predators of Gasterosteus, and that of the sticklebacks eaten, the majority were nine-spined sticklebacks. It thus appears that predation by fish is not a major source of mortality in three-spined sticklebacks at this location. This may explain the apparently high levels of infection. At Matamek Lake the temperature of the water is at a minimum of 4-5^{o}C for 7 or 8 months of the year. Under such continued adverse conditions any additional stress

greatly decreases the chances of survival. There is sufficient evidence in the literature to indicate that infection with Schistocephalus does cause stress to Gasterosteus, especially when infection levels are high. Consequently, it seems very probable that parasite-induced host mortality does contribute to the seasonal dynamics of the populations of Schistocephalus and Gasterosteus at Matamek Lake, although the manifestation of this phenomenon is undoubtedly distorted because of the non-random nature of the samples.

In some populations the appearance of small plerocercoids in sticklebacks (used as an indication of parasite recruitment) is reported to occur year round (Clarke, 1954; Pennycuick, 1971a). However, Pennycuick describes the peak of the infection as occurring in July. Hopkins and Smyth, (1951), Lester (1969) and Peacock (1979) also describe recruitment as occurring primarily in the summer months. At Matamek Lake parasite abundance was low in June and early July, increased most rapidly in late July and continued to increase throughout the sampling period in each year, indicating that recruitment commenced in July and continued for the rest of the sampling season.

Since a stickleback must eat an infected copepod to become infected, the characteristics of the infection in sticklebacks depend to a large extent on the population dynamics of the copepod and procercoid populations, and stickleback feeding habits. The most detailed description of the diet of G. aculeatus is presented by Hynes (1950) for three populations of sticklebacks in the U.K., however, several other authors have examined the stomach contents of sticklebacks from a wide

variety of habitats (Markley, 1940; Greenbank and Nelson, 1959; Maitland, 1965; Walkey, 1967; Abdel'-Malek, 1968; Valdez and Helm, 1971; Pope, 1973; Manzer, 1976; Reimchen, 1982). Some of the more common food items reported include diptera and chironomid larvae and pupae, oligochaetes, cladocerans, copepods, amphipods, ostracods, stickleback eggs and larvae and occasionally algae and higher plant materials. Seasonal variations in the composition of stickleback diets occur; these are frequently related to the seasonal abundance of food items. Sticklebacks are opportunistic in their feeding habits, feeding on whatever is most readily available. The composition of the diet is however limited by stickleback size, smaller fish are restricted to the smaller prey items, as they grow a wider range of potential prey becomes available to them. The relative contribution of copepods to the diet of sticklebacks varies between populations. Markley (1940), Maitland (1965), Pope (1973) and Reimchen (1982) describe copepods as being of little importance, whereas Hynes (1950), Greenbank and Nelson (1959), Valdez and Helm (1971) and Manzer (1976) describe copepods as being very important in the diet of Gasterosteus. It is difficult to make a quantitative comparison of the results presented by these authors because the methods used to indicate the relative importance of food items vary between studies (see Hynes (1950) for a discussion of the different methods used) and samples for analysis have been collected at different times of the year. In general however, copepods, and other small items such as cladocerans, predominate in the diet of small sticklebacks whereas, larger items, such as insect larvae and

pupae, predominate in the diet of large individuals. Although copepods do not comprise a major component of the bulk of the stomach contents of older sticklebacks they are found, and the probability of a fish becoming infected with Schistocephalus is related to the number of copepods ingested. At Matamek Lake, a small number of 3++ fish contained single small plerocercoids suggesting that these worms were recently acquired. The increase in prevalence and mean parasite intensity with host size, reported for several populations of sticklebacks (Chappell, 1969b; Gilbertson, 1980; Reimchen, 1982) also suggests that older fish continue to pick up new infections. Abdel'-Malek (1968) reported that stickleback fry feed almost exclusively on copepod nauplii and copepodite stages, thus sticklebacks may become infected in their first year of life. The extent to which fry become infected probably depends on the relative timing and length of the stickleback spawning season and of the period when copepods contain infective procercoids. Pennycuick (1971b) found that 79% of 0+ fish collected at Priddy Pool were infected with Schistocephalus ($\bar{x}$=3.0). In the present study the maximum prevalence found in 0+ fish was 18% ($\bar{x}$=1.0). Although the major period of recruitment commenced in July at both locations, spawning occurred as early as May at Priddy Pool as compared to late June at Matamek Lake, and it is probable that the fry at Matamek Lake did not start to feed on copepodites until late in the season. In addition, further recruitment also occurred during the winter at Priddy Pool which may account for the higher infection levels in fry at this location.

Diaptomus minutus and Cyclops scutifer are two of the

most abundant zooplankton species which occur at Matamek Lake. Since several related species of Diaptomus and Cyclops are recorded as being suitable fish intermediate hosts (Hopkins and Smyth, 1951; Clarke, 1954; Dubinina, 1957; Orr and Hopkins, 1969), it seems likely that one (or both) of these two species acts as the intermediate host for procercoids of Schistocephalus at Matamek Lake. The seasonal changes in abundance of these two cyclopoid copepods at Matamek Lake, in 1970, are described by Pope (1973). Boers and Carter (1978a,b) examined the life histories of these two species at Lake C22 (locally known as Facile Lake), which lies approximately 3km northeast of Matamek Lake (see Figure 1). Although C22 is considerably smaller than Matamek Lake and probably warms up more rapidly in the spring, the limnological characteristics of all the lakes in the Matamek watershed are very similar (Pope, 1973), and it seems likely that the life histories of D. minutus and C. scutifer would be similar at the two locations.

Copepodids are more frequently infected than mature forms of copepods (Clarke, 1954). Since procercoids take 2-4 weeks at 17°C to develop to infectivity (Clarke, 1954; McCaig and Walkey, 1964) and small worms are not found in sticklebacks in any abundance until mid and late July, we can assume that the copepods start to become infected in late June. This correlates well with the occurrence of peak densities of cyclopoid copepodids in late June (Pope, 1973) and more specifically with peak densities of copepodids of Cyclops scutifer and Diaptomus minutus in June and July, described by Boers and Carter (1978a,b). These authors also reported that copepodids of these

two species were found until late September when the last sample was collected. Eggs take approximately 4 weeks to hatch at 18-19°C (Clarke, 1954), thus we may assume that the eggs which ultimately gave rise to the small plerocercoids seen in July first start to develop in late May following ice-out.

When an infective plerocercoid is eaten by a piscivorous bird, egg production commences within 36 hours, the adult worm only spends 3-4 days in the definitive host (Hopkins and Smyth, 1951). Thus it is conceivable that the small plerocercoids seen in July may be the offspring of those eaten by piscivorous birds at the end of May. Alternatively, the eggs may have accumulated in the lake as a result of predation in the fall and remained dormant over winter to hatch in the spring. Thomas (1947) describes increasing temperature and light intensity as providing suitable stimuli and conditions for development and hatching of eggs of Schistocephalus. It seems feasible that if the conditions are not favourable for development in the autumn, then development may be prevented until conditions improve in the spring. Many other species of invertebrates, including copepods, have resting stages which enable them to survive the winter. Clarke (1954) reported that one batch of Schistocephalus eggs collected in May, when kept in vitro, continued to produce coracidia for 6 months, although the majority hatched within the first few weeks. The overwintering of Schistocephalus eggs could provide the parasite with an efficient means of ensuring that the hatching of eggs coincides with the maximum abundance of suitable copepodids.

A further point worth mentioning is that infected

copepods have been reported to live for three months (Clarke, 1954). Elgmork (1959) and Cole (1955) (both cited by Watson and Lawler, 1965) described the life cycles of two species of Cyclops, and noted that a proportion of the copepods descend to the sediments and pass the summer in a dormant condition in the IV copepodite stage. If procercoids are able to survive in resting copepodites then the longevity of the infective procercoid will be increased, thus increasing the probability of transmission to a stickleback host and possibly accounting for a period of recruitment later in the season. At present, field data regarding the biology of Schistocephalus outside the three-spined stickleback is lacking. Until the situation is rectified such hypotheses remain purely speculative.

One of the most striking characteristics of Schistocephalus is the large size attained by the plerocercoids in the stickleback host. Since the plerocercoids apparently live and continue to grow for as long as their fish hosts, the size attained by plerocercoids depends partially on the longevity of the host. McCaig and Hopkins (1965) reported that the largest plerocercoid they found weighed 93 mg (dry weight). In the present study most of the parasites weighed less than 80mg (dry weight,) however a small proportion were larger, the largest weighing 128 mg (dry weight). This plerocercoid was found in the largest fish collected, a female measuring 78 mm and it seems likely that this individual may have been older than most of the others in the sample. Pennycuick (1971b) describes finding a plerocercoid of 0.62g (fresh weight) in a 3+

fish. Using the conversion factor for worms weighing over 0.1g, given by McCaig and Hopkins (1965) (dry weight/wet weight=33%, the dry weight of this very large worm is estimated at 200mg. The only other cestode which exhibits such extensive somatic growth in its intermediate host is Ligula intestinalis.

In vitro growth studies of plercercoids are described by McCaig and Hopkins (1965) and Sinha and Hopkins (1967). Growth is slow between 4 and 7°C, between 7 and 23°C the growth rate increases exponentially, maximum growth occurs between 23 and 27°C, and above 27°C the growth rate declines. (Water temperatures above 22°C would rarely, if ever be experienced in the field.) The growth and consequent pathological effects of plerocercoids of Schistocephalus on Gasterosteus are thus temperature related. The differences in the temperature regime experienced by populations of Schistocephalus throughout the range of the species may account for some of the observed variation in infection patterns as a direct result of the effect of temperature on worm growth. Growth is not only related to temperature but also to plerocercoid size; the growth rate of a plerocercoid of double the weight of another has approximately half the specific growth rate (McCaig and Hopkins (1965). This phenomenon made it difficult to compare growth rates found in the field with those from in vitro and in vivo growth studies, because plerocercoid sizes in addition to temperatures needed to be comparable. The majority of the experiments were carried out on worms less than 20mg, whereas most of the data available from Matamek Lake for the analysis of worm growth, involved larger worms. In only one instance were direct comparisons feasible.

From data presented by McCaig and Hopkins (1965) it can be estimated that after 16 days at approximately 22°C a plerocercoid of original dry weight of 8mg weighed 27mg (dry weight). The mean dry weight of plerocercoids from single infections at Matamek Lake in mid July 1982 was also 8 mg. After 14 days at an approximate water temperature of 21°C (at a depth of 1m) the mean dry weight of plerocercoids was 26.5mg. It thus appears that in vitro and in vivo growth may be similar, but further, more extensive comparisons should be made before arriving at a conclusion.

Following the surgical techniques of Bråten (1966), Meakins and Walkey (1973) surgically transplanted plerocercoids of known weight into uninfected fish, and subsequently monitored plerocercoid growth in single, double and five worm burdens. They were able to affirm and quantify the observations of earlier authors (Vik, 1954; Orr and Hopkins, 1969; Lester, 1971) that depression of growth occurs in multiple infections, the extent of the depression increasing with higher numbers of worms. This phenomenon also occurred in sticklebacks at Matamek Lake; both the mean plerocercoid weight and the weight of the largest plerocercoid per fish decreased as the parasite intensity increased. This phenomenon is widespread in helminth infections, especially in cestode populations where it is more frequently referred to as the "crowding effect" (after Read, 1951). The majority of references to this effect come from studies on Hymenolepis spp. (Read, 1951; Roberts, 1966; Jones and Tan, 1971; Moss, 1971; Ghazal and Avery, 1974; Hesselberg and Andreassen, 1975; Befus, 1975) and Diphyllobothrium spp.

(Andersen, 1972; Halvorsen and Andersen, 1974) in avian and mammalian definitive hosts. There are very few reports of crowding effects within intermediate hosts, although there is evidence that the growth rate of cestode procercoids in copepods may be density-dependent (Rosen and Dick, 1983).

From maturation studies Hopkins and McCaig (1963) reported that it takes three months at 19°C for plerocercoids to attain a fresh weight of 50mg (approximately 14mg dry weight) and to become fully infective to ducklings. Maturation may occur in smaller worms, but, evidence suggests that the smaller worms are less able to retain their position in the intestine of the definitive host than larger ones. In October 1981, plerocercoids ranging from <1mg to almost 100mg (dry weight) were found in 1+ sticklebacks, the major proportion weighing between 10 and 40mg. It thus appears that most of the plerocercoids at Matamek Lake are potentially able to infect an avian host and complete the life cycle within three months of a stickleback becoming infected, despite density-dependent growth. In worm burdens of low intensities, growth and development to infectivity and to a state of readiness to mature may be achieved within a shorter time period. It should be noted, however, that Hopkins and McCaig used chickens and ducklings which were only several weeks old in their studies because the proportion of plerocercoids which became established decreased in older birds.

In the present investigation, the Parasite Index increased with increasing parasite numbers and then reached a plateau. Moss (1971) and Ghazal and Avery (1974) observed

similar relationships between total parasite biomass and parasite intensity for Hymenolepis microstoma and Hymenolepis nana in the intestines of their respective hosts. They attributed these relationships to density-dependent growth of the parasites resulting from competition for limited resources. Although density-dependent growth undoubtedly plays a role in determining the form of this relationship in Schistocephalus populations, other factors may be involved. There is strong evidence to indicate that high infection levels do cause stickleback mortality and it is possible that the plateau at a Parasite Index of 45% represents an approximate lethal level of parasitaemia to sticklebacks at this time of year such as that described by Crofton (1971). Individual variations are to be expected, but in general, parasite growth beyond this threshold value may result in host mortality. If this is the case, the value at which the P.I. reaches a plateau would obviously vary in response to environmental conditions, such as temperature and food availability.

It is not known what resource is limiting to the growth of plerocercoids in sticklebacks. Evidence presented previously indicates that plerocercoids do compete with their hosts for energy resources, and it is possible that a specific nutrient is limiting. From the examination of heavily infected sticklebacks it is immediately apparent that the plerocercoids are very tightly packed together in the abdominal cavity. Thus, it is also possible that it is not the host supply of nutrients that is limiting per se, but, that the uptake of nutrients over the surface of plerocercoids is impeded because physical space is

restricted.

CHAPTER VI - OVERVIEW

From the analysis of stickleback size frequency distributions it is estimated that three-spined sticklebacks, Gasterosteus aculeatus, at Matamek Lake, Quebec, live for at least three years. In general, females mature for the first time in the spring following their third winter of life, at the age of 3+. Breeding takes place in June and early July.

The highest infection levels with Schistocephalus solidus were found in 1+ fish. It is likely that this results directly from stickleback feeding habits because copepods generally comprise a major proportion of the diet of young sticklebacks, whereas larger fish prefer larger food items. Infection in the young of the year is probably limited by their size, with only a few attaining a large enough size in their first year to feed on this food source.

The major period of parasite recruitment commenced in late July, at a time when copepods are very abundant (Pope, 1973; Boers and Carter, 1978a,b) and warm temperatures are conducive to fish feeding and rapid growth. It is proposed that the July recruits were offspring from eggs which started to develop at ice-out. It is not known whether these eggs accumulated in the autumn and remained dormant over winter, or whether they were deposited by piscivorous birds feeding on infected sticklebacks in late May/early June. In either case, the onset of embryonation at this time would result in the release of coracidia in late June, simultaneous with the first

peak in copepod density (Boers and Carter, 1978a,b). Recruitment continued throughout the ice-free period. By the end of October 1981, the prevalence and mean intensity of 1+ sticklebacks had reached values of 100% and 6.8(1-25) respectively. The 2+ age class was apparently absent in June 1982 and poorly represented in June 1983, but the limited data indicate a huge drop in the level of infection in the 1+ cohort over the winter, to a prevalence of 5% and a mean parasite intensity of 1.0 in the spring. Although the absence of a 2+ year class may be explained in terms of spatial segregation of different age classes of sticklebacks, and the change in the infection level can be attributed to the changing spatial distribution of the uninfected and infected sticklebacks in the population, it seems likely that selective mortality of heavily infected sticklebacks occurred over the winter.

This assumption is based on the following evidence. First of all, the mean Parasite Index of 1+ sticklebacks in October 1981 was 43.8%, considerably higher than that of dead fish (mean P.I.=36%) collected by Pennycuick (1971b) during the winter at Priddy Pool in England. Secondly, in the small proportion of 2+ and 3++ sticklebacks which were infected, the parasite intensity did not exceed 5. In contrast, multiple infections of up to 40 plerocercoids were found in 1+ fish. Since plerocercoids are not lost from sticklebacks, the drop in the infection level between age classes probably reflects the loss of heavily infected individuals from the population. Mortality rates of infected sticklebacks are reported to increase when the fish are exposed to other stresses (see

previous chapter for details), and thus it is likely that parasite-induced mortality would occur predominantly during the winter months when food is scarce. In addition, infection data of young of the year indicate that selective mortality of infected fry also occurred during this period. The selective mortality of heavily infected hosts has been proposed to occur in other cestode infections of intermediate hosts: procercoids of Triaenophorus crassus in copepods, Cyclops bicuspidatus thomasi, (Rosen and Dick, 1983); cysticercoids of Hymenolepis diminuta in the flour beetle, Tribolium confusum, (Keymer, 1980); plerocercoids of Diphyllobothrium spp. in Arctic char, Salvelinus alpinus (Henricson, 1980; Curtis, in press); plerocercoids of Triaenophorus nodulosus in burbot fry (Lopukhina et al., 1973).

It has been suggested that infection with Schistocephalus solidus predisposes sticklebacks to predation since the abdominal distension of the host caused by heavy parasite burdens apparently impairs their swimming ability and makes them more easily visible (Clarke, 1954; Arme and Owen, 1967; Coad and Power, 1973). In addition, Giles (1983) found that infected sticklebacks recover more quickly from a frightening overhead stimulus than do non-parasitized individuals. There are several examples of the modification of the behaviour of intermediate hosts by parasites (Holmes and Bethel, 1972). When such modifications make the host more susceptible to predation by the definitive host, parasite transmission is enhanced. If, however, the behavioural changes also make the intermediate host more susceptible to predators which do not serve as definitive hosts,

then the chances of survival of both the host and parasite decrease.

At Matamek Lake three-spined sticklebacks were not found to be an important food item to the piscivorous fish species present (Pope, 1973), thus it appears that predation by unsuitable hosts is not a major source of mortality of sticklebacks at this location. This may account for the high infection levels observed.

Infection with S. solidus was found to retard host growth. In general, infected 3++ females did not mature, even when only a single plerocercoid was present. The only gravid, infected female found had apparently failed to spawn.

Density-dependent growth of plerocercoids was exhibited in multiple infections. Thus it was not possible to differentiate between plerocercoids of different age on the basis of their size. However, data on single infections indicated that few plerocercoids live for more than one year in sticklebacks at Matamek Lake. The importance of crowding on differentiation of larval forms is not well understood and is frequently overlooked as a factor in transmission. In a recent study, Rosen and Dick (1983) showed that intensity of infection of Triaenophorus crassus in Cyclops bicuspidatus thomasi affects host longevity and procercoid growth, differentiation, and infectivity. Results of the present study indicate that infection with plerocercoids of S. solidus affects stickleback longevity. Since plerocercoids must attain a certain size to become infective to piscivorous birds it is is possible that density-dependent growth of the plerocercoids does reduce the

transmission of the parasites to the final host. Kennedy (1976) suggests that intraspecific competition between parasites in an individual host may be a mechanism in regulating parasite populations. Until more is known about the size at which plerocercoids become infective and are able to mature in the definitive hosts, it is not possible to determine whether or not density-dependence actually operates as a control mechanism in regulating the size of Schistocephalus populations. Regulation of parasite populations may also occur by death of heavily infected hosts when the parasites are overdispersed within the host population (Crofton, 1971). The data presented here indicate that selective mortality of infected sticklebacks does occur and it is probable that this serves to regulate parasite numbers.

Parasites can regulate the population dynamics of the host through effects on survival and reproduction (Anderson, 1979). Infection with S.solidus does affect the survival and breeding success of sticklebacks, and on these grounds, Pennycuick (1971d) proposes that Schistocephalus causes cyclic fluctuations in both its own and the host populations. In the present study it was found that only the uninfected females matured and bred. Thus it appears that only the proportion of the population which manage to escape the infection are able to propagate the population. Whether or not Schistocephalus actually regulates host numbers depends on whether this proportion is smaller than that which would normally reproduce in an uninfected population. Holmes (1982) suggests that in many cases host mortality due to parasites may be compensatory rather

than additive to other sources of mortality, and thus parasites may not play such an important role in regulating host populations. In the absence of comparative quantitative data on stickleback abundance and the reproductive potential of infected and uninfected populations, it is not yet possible to determine what part Schistocephalus may play in regulating the population dynamics of sticklebacks.

McPhail and Peacock (1981) studied a population of three-spined sticklebacks in B.C. The sticklebacks exhibited a life span of a little over two years, with females maturing for the first time when one year old. Infection levels in samples composed of 1+ and 2+ fish were low during the breeding season and increased over the summer. These authors hypothesize that selection has acted upon Schistocephalus populations and as a result the adverse effects of plerocercoids on sticklebacks are delayed until after the host has reproduced. At Matamek Lake many sticklebacks became very heavily infected in their second year of life and only the surviving uninfected 3++ females showed signs of maturity. These findings do not support McPhail and Peacocks hypothesis.

It appears that the infection dynamics of S. solidus in G. aculeatus depend largely on environmental constraints such as the availability of other hosts in the life cycle, predation pressure and the temperature and photoperiod regime. In addition, the genetic heterogeneity of the host species may contribute to the observed variability of infection patterns through differences in the life history and behaviour of different stickleback genotypes.

Schistocephalus may exert regulatory effects on its own population size and that of its host, but the extent to which this actually occurs will depend on the interaction of many of these internal and external factors.

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APPENDIX

Figure 1. Cumulative length frequency distribution for sticklebacks collected on 30.6.82 plotted on probability paper (●). The distribution comprises two curves connected by a point of inflexion, indicating that the distribution is bimodal. The two component curves are replotted separately (○). By fitting a line through these points the mean and 90% confidence limits of each of the two modes can be estimated.

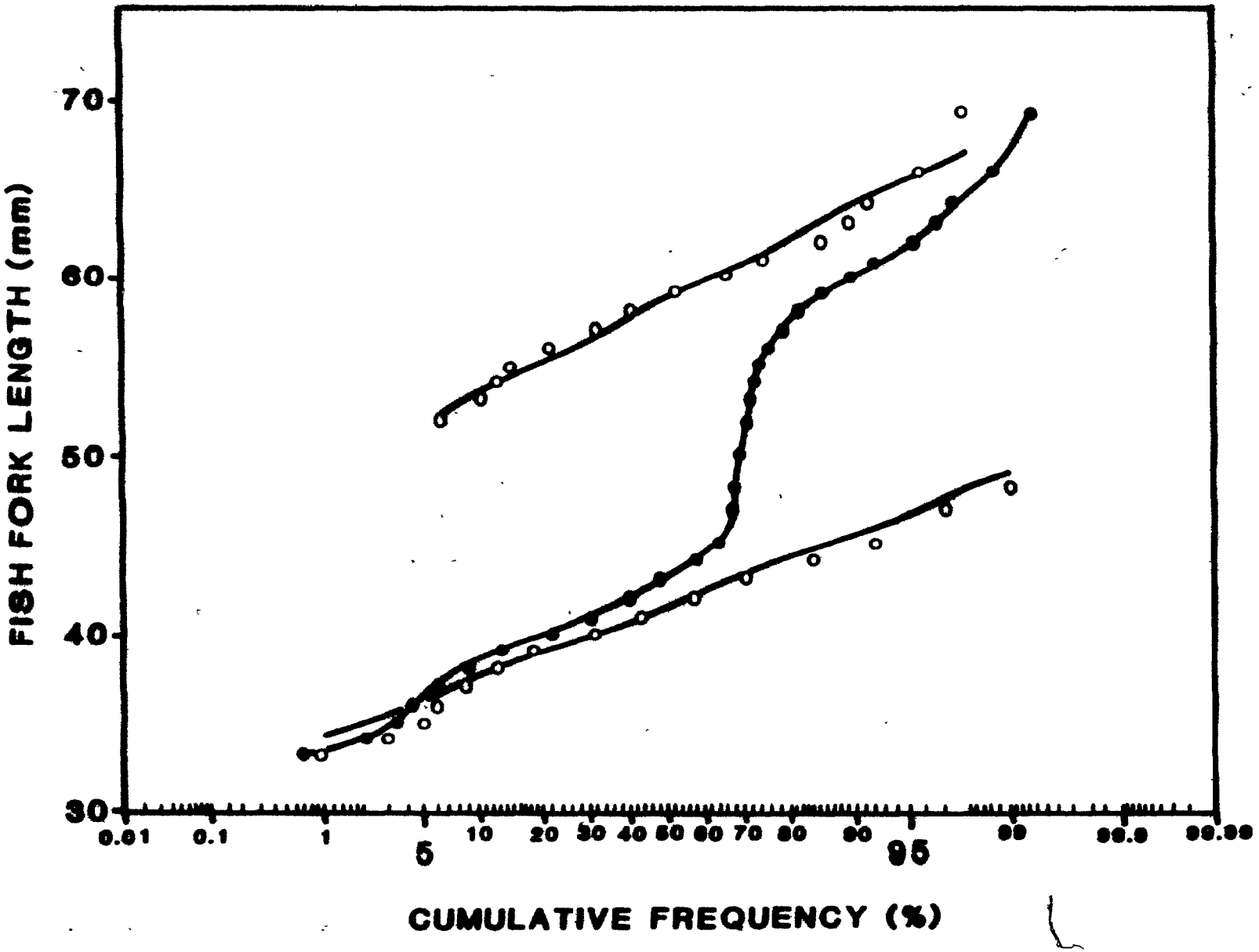
FISH FORK LENGTH (mm)
70
60
50
40
30
0.01
0.1
1
5
10
20
30
40
50
60
70
80
90
95
99
99.9
99.99
CUMULATIVE FREQUENCY (%)

Figure ii. Length frequency distributions of male and female sticklebacks collected at the South camp, July 1981.

A. Both sexes combined (n=175).

B. Females (n=80).

C. Males (n=89).

(It was not possible to sex six of the fish.)

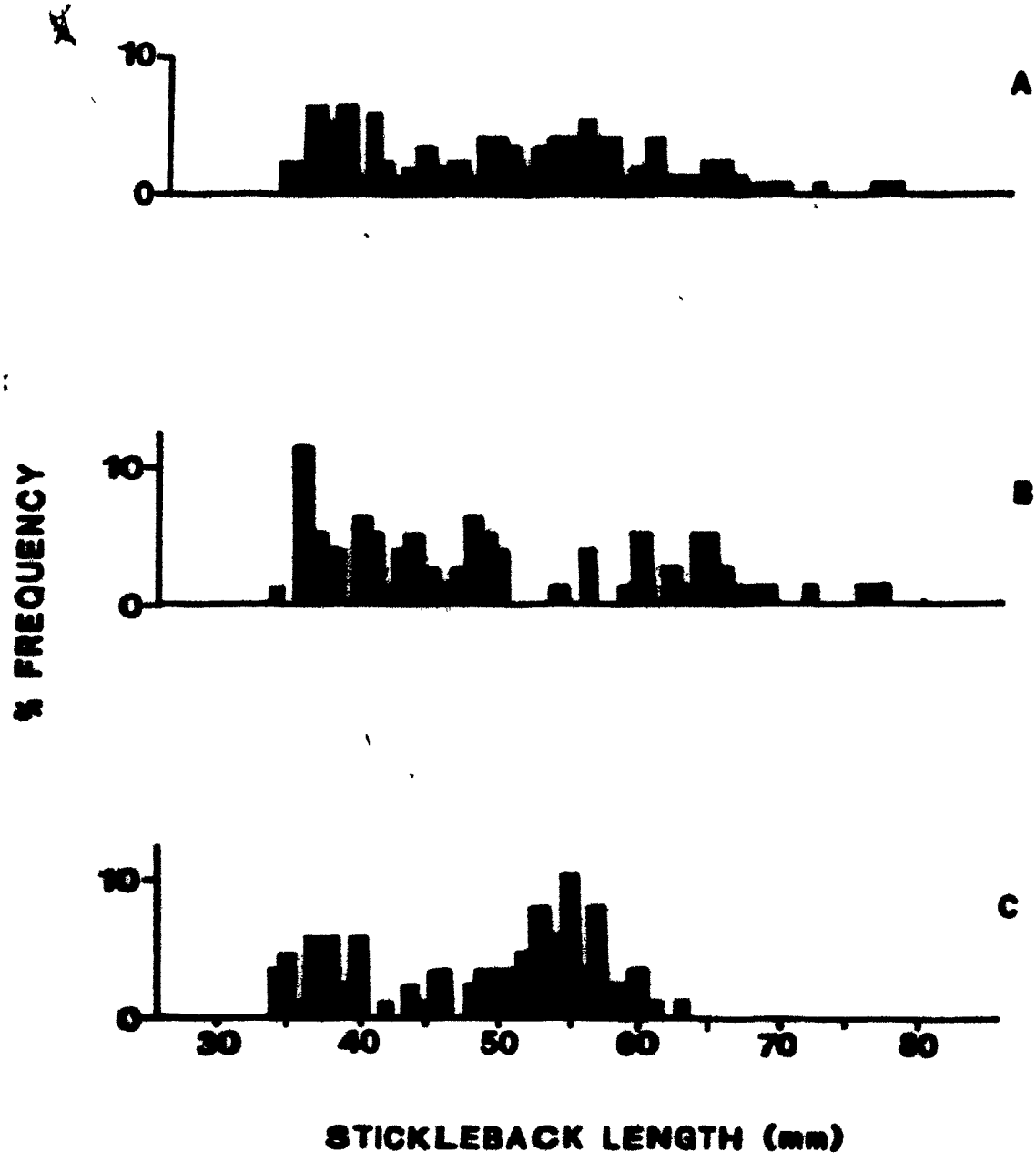
10
0
A
10
0
B
% FREQUENCY
10
0
C
30
40
50
60
70
80
STICKLEBACK LENGTH (mm)

Figure iii. Relationships between mean plerocercoid weight, mean weight of the largest plerocercoid per fish, mean Parasite Index and parasite intensity for 1+ sticklebacks collected in September (A–C) and October (D–F) 1981. All fish containing plerocercoids weighing <4.5 mg dry weight were excluded. Sample sizes are given above the points in plots A and D.

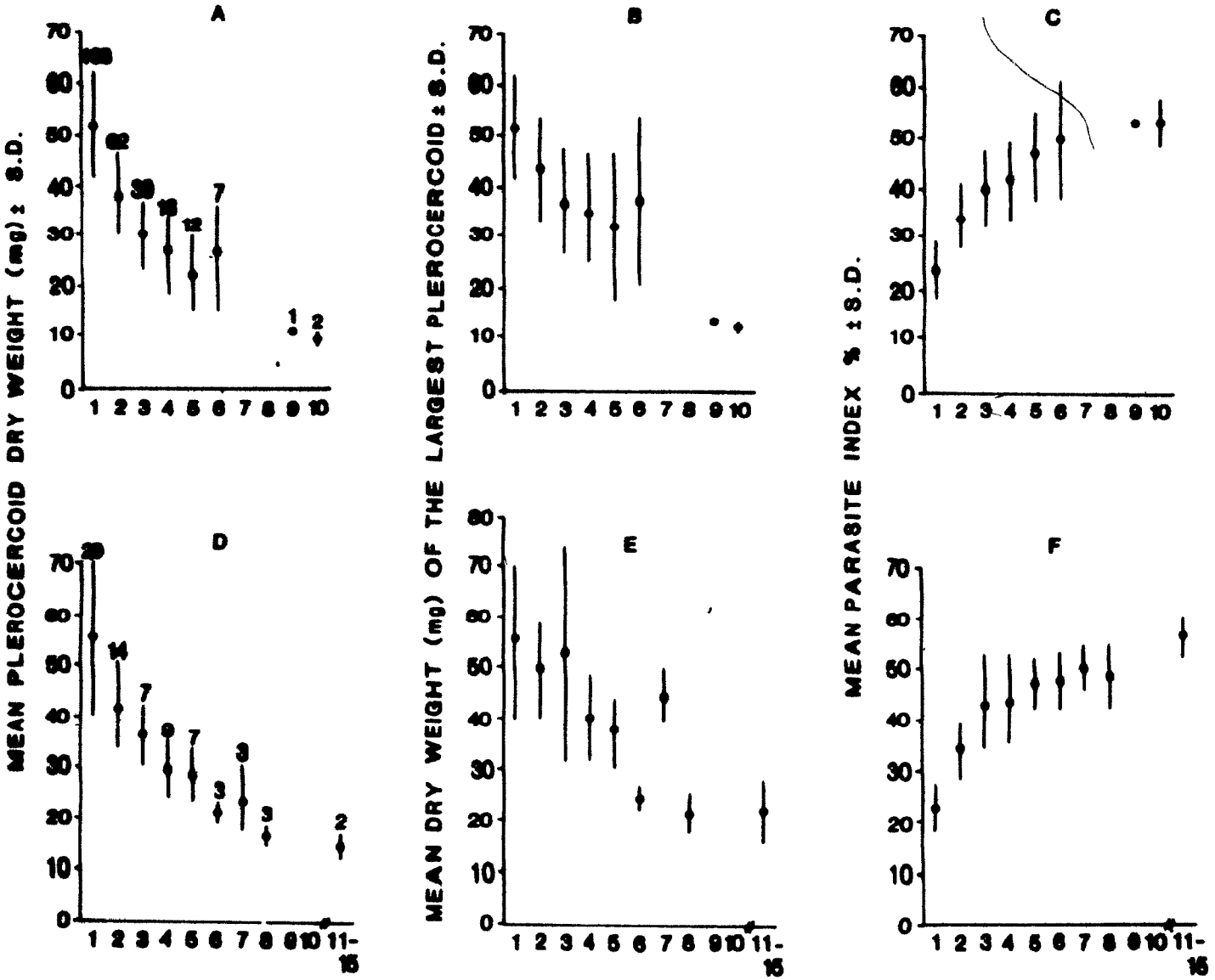
A
B
C
D
E
F
MEAN PLEROCERCOID DRY WEIGHT (mg) ± S.D.
MEAN DRY WEIGHT (mg) OF THE LARGEST PLEROCERCOID ± S.D.
MEAN PARASITE INDEX % ± S.D.
NUMBER OF PLEROCERCOIDS PER FISH

Figure iv. Frequency distributions of the weights of plerocercoids of S. solidus from infections of different intensities. Only plerocercoids from 1+ sticklebacks collected in October 1981 are included.

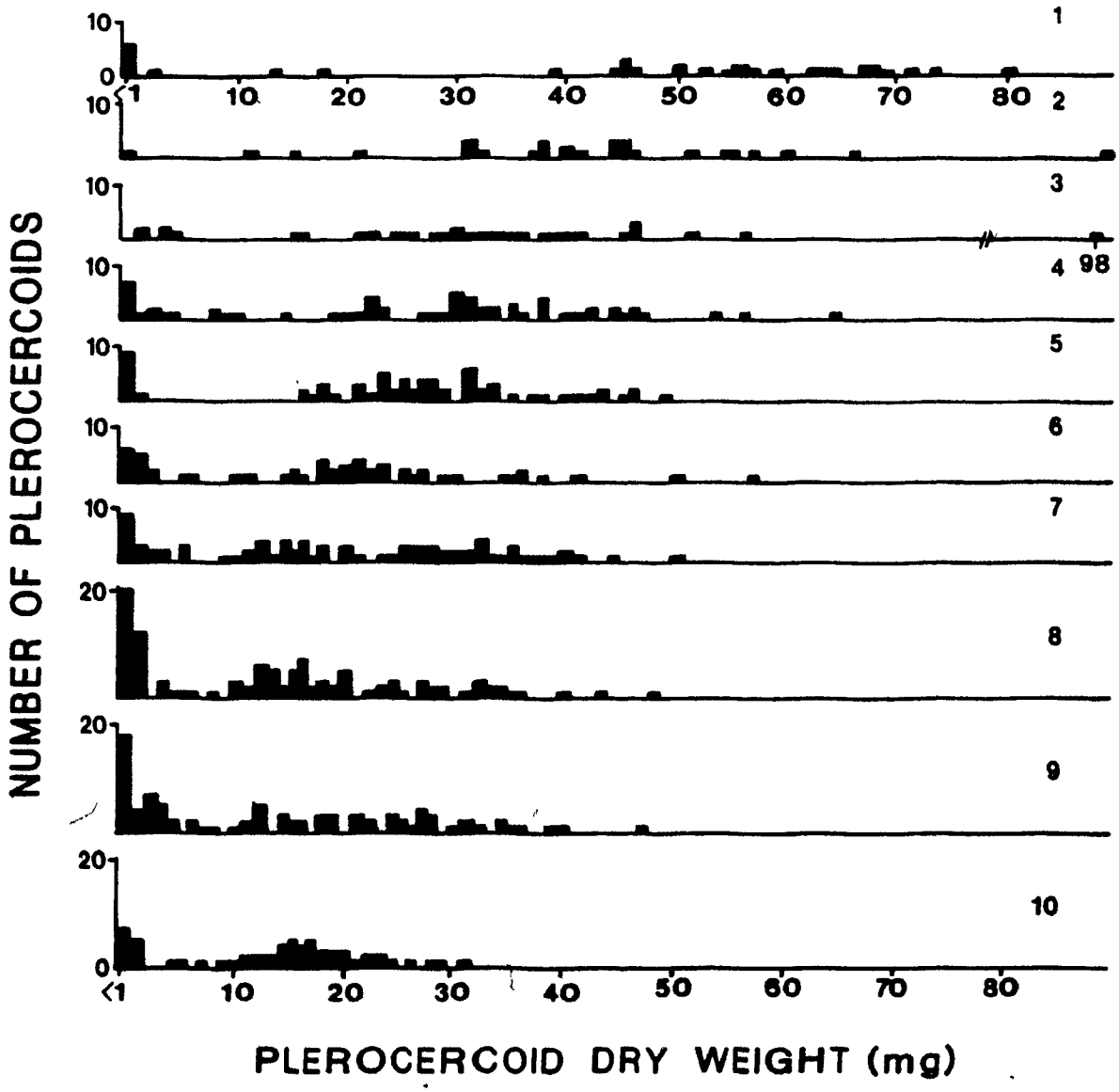
NUMBER OF PLEROCERCOIDS
PLEROCERCOID DRY WEIGHT (mg)
1
2
3
4
5
6
7
8
9
10
98
<1
10
20
30
40
50
60
70
80

Table 1. Seasonal infection data for all samples of sticklebacks, irrespective of age, collected at Matamek Lake, Quebec.

Date	Sample size	Prevalence %	Mean parasite intensity (range)	Parasite Index % Mean	Min.	Max.
South Camp						
9.7.81	170	71.8	5.4 (1-23)	25.1	0.1	60.3
1.8.81	66	90.9	3.6 (1-10)	28.6	0.2	47.9
18.8.81	151	100.0	4.7 (1-22)	34.1	0.1	57.0
28.8.81	198	100.0	5.9 (1-29)	35.4	15.8	53.8
North Camp						
16.8.81	129	99.2	4.3 (1-24)	37.6	0.1	60.9
11-13.9.81	157	93.6	5.3 (1-40)	34.8	12.9	60.5
29-30.10.81	230	79.6	6.8 (1-25)	40.9	0.1	63.7
16.6.82	100	6.0	1.0	19.3	4.0	32.8
30.6.82	149	2.0	1.0	4.5	0.1	12.4
14.7.82	160	11.3	1.3 (1-3)	8.9	0.1	24.6
28.7.82	92	58.7	1.5 (1-6)	23.1	0.8	46.7
11.8.82	164	68.3	1.6 (1-6)	28.2	5.4	50.4
25.8.82	165	89.1	1.8 (1-8)	30.3	12.2	55.6
12.6.83	150	4.7	1.0	19.1	0.2	29.8

Table ii. Seasonal infection data for specific age classes of sticklebacks collected at the North Camp of Matamek Lake, Quebec.

Date	Age	Sample size	Prevalence %	Mean Parasite intensity (range)	Mean Parasite Index %
16.8.81	1+	117	100.0	4.0 (1-19)	37.4
11-13.9.81	0+	8	0.0		
	1+	129	100.0	5.3 (1-40)	34.8
29-30.10.81	0+	50	18.0	1.0	6.3
	1+	143	100.0	7.3 (1-25)	43.8
16.6.82	1+	63	3.2	1.0	13.6
	3++	24	12.5	1.0	18.6
30.6.82	1+	89	1.1	1.0	0.1
	3++	43	2.3	1.0	12.4
14.7.82	1+	121	11.6	1.2 (1-3)	8.5
	3++	21	14.3	2.0 (1-3)	14.1
28.7.82	1+	71	63.4	1.4 (1-6)	23.0
	3++	10	30.0	1.7 (1-3)	17.0
11.8.82	1+	133	70.7	1.6 (1-6)	29.0
	3++	10	30.0	2.3 (1-5)	20.9
25.8.82	0+	12	0.0		
	1+	139	97.8	1.7 (1-7)	30.6
12.6.83	1+	52	3.8	1.0	0.2
	2+	13	7.7	1.0	26.9
	3++	62	3.2	1.0	27.2

Table iii. Paired dry weights of plerocercoids from 1+ sticklebacks harbouring double infections, collected on 11-13.9.81 at the North Camp of Matamek Lake.

Type "A" infections		Type "B" infections		Type "B" infections cont'd.	
Plerocercoid dry weights (mgs)		Plerocercoid dry weights (mgs)		Plerocercoid dry weights	
62.9	0.1	50.7	37.9	32.2	20.9
46.5	2.3	55.2	54.7	45.0	31.6
69.3	2.4	26.6	23.8	34.5	44.0
49.6	0.9	48.3	35.0	35.4	32.2
48.1	0.8	41.2	17.1	44.7	35.2
51.6	0.5	63.5	57.8	35.4	37.9
51.0	0.9	35.9	27.1	44.7	35.2
51.6	1.5	56.3	49.6	35.4	37.9
40.5	0.1	49.1	20.0	40.8	28.7
44.9	0.3	53.9	33.6	31.6	32.9
29.8	0.1	46.4	42.0	54.3	51.3
71.8	1.2	42.7	34.2	38.1	39.8
43.1	0.1	51.5	37.8	60.6	43.8
51.2	0.2	53.6	55.5	44.1	30.9
50.0	0.6	40.9	42.3	38.2	31.2
		38.6	21.8	51.2	49.6
		50.5	33.6	50.4	27.3
		45.7	42.0	44.0	20.3
		41.8	44.4	44.2	34.4
		37.6	39.9	47.8	44.1
		48.6	55.9	46.4	32.9
		29.9	30.9	50.4	32.0
		44.3	32.6	32.1	25.4
		32.1	25.5	38.1	22.0
		60.8	34.4	32.2	20.8
		73.2	13.9	24.8	21.8
		43.7	58.7	33.8	22.7
		22.9	34.2	38.8	27.8
		63.3	29.9	31.7	28.6
		37.5	54.9	29.5	29.0
		35.7	31.8	36.6	24.6
		30.9	30.5	30.7	26.1
				35.2	22.2

Table iv. Wet weight/dry weight ratios for eviscerated sticklebacks, their ovaries and plerocercoids of *Schistocephalus solidus*, stored in 70% alcohol.

	Ratio of wet wt./dry wt.	Dry wt. (mg) Max.	Min.	n	r	p
Eviscerated sticklebacks	3.27	729.6	30.7	150	0.999	0.0001
Ovaries	3.40	94.0	0.1	86	0.997	0.0001
Plerocercoids	3.09	70.4	0.1	7	0.998	0.0001