Spring 1978

STUDIES ON THE PARASITES OF SMOOTH FLOUNDER LIOPSETTA PUTNAMI (GILL) IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

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7824543

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STUDIES ON THE PARASITES OF SMOOTH FLOUNDER LIOPSETTA PUTNAMI (GILL) IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE.

UNIVERSITY OF NEW HAMPSHIRE, PH.D., 1978

STUDIES ON THE PARASITES OF SMOOTH FLOUNDER *LIOPSETTA PUTNAMI* (GILL) IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

by

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A THESIS

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Doctor of Philosophy

Graduate School

Department of Zoology

May, 1978

This thesis has been examined and approved.

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April 14, 1978
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ACKNOWLEDGEMENT

I'd like to thank the members of my committee, Drs. Robert Croker, Galen Jones, Philip Sawyer, and Richard Strout, for their support and editorial assistance. My special gratitude goes to my major professor, Dr. Wilbur L. Bullock, who provided more than an education in parasitology, and to my wife, Lisa, who came through with flying colors.

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ABSTRACT

Young-of-the-year and yearling smooth flounder (Liopsetta putnami) were seined during 1974-1976 from the Great Bay estuary, New Hampshire, to study parasite seasonal abundance and maturation cycles, habitat specificity, frequency distributions, interspecific correlations, and age related differences between hosts. Twenty seven species of parasites (7 Protozoa, 20 Metazoa) were found, including 24 new host records. The only common parasites not showing seasonal periodicity were Zoogonus lasius (Digenea) and Cryptobia bullocki (Protozoa).

The parasites varied in habitat specificity, which was mediated primarily by active site selection. Most intestinal helminth populations were more evenly distributed in higher intensity infections. The monogenean Protancyrocephaloides liopsettae formed conspicuous aggregations, most commonly on the ventral portion of the first, left, gill arch.

Parasite frequency distributions were overdispersed, and where numbers permitted, were best described by the negative binomial. Significant Spearman's rank correlation coefficients were found between several species pairs; the most frequent a positive one between Lepocreadium setiferoides and Zoogonus lasius. The biological reason for such correlations is unclear.

Lepocreadium setiferoides, Zoogonus lasius, Cryptocotyle lingua, and Cryptobia bullocki were more abundant in 1+ age group flounder. Lecithaster confusus was less abundant in older fish, probable because it consumed fewer copepod intermediate hosts. Differences in parasitism between 0+ age group hosts in 1975 and 1976 were described as the natural variation of unregulated populations.

A comparison of hosts maintained in the laboratory for up to four days showed the position and intensity of most intestinal helminth infections changing significantly after one day, and prevalence after two days. The most probable reason for these changes was th eloss of food from the gut. Histozoic protozoa and encysted helminths did not change in abundance over the study period.

Smooth flounder parasites from two contrasting habitats in the estuary were compared to illustrate the effect of environment on a parasite fauna, and to study possible mixing of fish stocks. Differences in some parasite species, as well as in abundance and maturity of other infections, indicated a lack of intermixing. Changes in helminth diversity indices corresponded to those in the free-living communities of the two areas. The use of these indices is examined as a method for separating fish stocks, and as possible indicators of environmental quality.

Smooth flounder and winter flounder (Pseudopleuronectes americanus) parasites from one collecting site were compared to study their host specificity and to determine the extent of competition between flounder species. Parasites differed in abundance and relative maturity, and indicated probable differences in host diets. Comparison of helminth diversity indices between hosts was inconclusive, giving different results for different sampling periods.

The value and weaknesses of field oriented population biology studies are discussed.

PART I

General Introduction

According to Margolis (1965), the composition of the parasite fauna of any host is the result of two types of factors. First are the ecological influences, the biotic and abiotic characteristics of the habitat which determine the possibilities for contact between parasite and host. Secondly, there are evolutionary factors, the sum of physiological and morphological adaptations, of both parasite and host, which allow contact to be maintained. An understanding of these factors helps us to interpret the significance of a parasitic infection. Such an infection is the result of discrete and predictable processes, including specific parasite life cycles and preferred habitats of intermediates. When these are known, the presence of a parasite provides information about the host, the parasite, and the ecosystem in which both have functioned.

The purpose of this study has been to investigate the parasites of smooth flounder, Liopsetta putnami (Gill), in the Great Bay Estuary, New Hampshire, both in terms of the population dynamics of the parasites and what we can infer from them about the flounder and its estuarine habitat. The smooth flounder is a common estuarine species which is often confused with the winter flounder (Pseudopleuronectes americanus). Neither the parasites nor the general life history of the smooth flounder are well known.

Although the older literature contains some good general parasite population studies (e.g. Ward, 1912; Van Cleave and Mueller, 1934), recent years have seen an increased emphasis on such investigations.

MacKenzie and Gibson (1970) provide an outstanding example of this type of work, and one of the few dealing with the parasites of marine fish species. The most common tendency has been to concentrate on one parasite species (Spall and Summerfelt, 1970; Boxshall, 1974; Stromberg and Crites, 1975; Anderson, 1976) rather than the entire parasite-mix of a given host. Studies having a slightly broader viewpoint include those of Pennycuick (1971 a, b, c), Davis and Huffman (1975), and Rawson (1976). These papers deal with one group of parasites, such as the helminths, but there is no long term ecological study of the entire parasite fauna of an estuarine fish species. Such a study for the smooth flounder would include year round prevalence and intensity of all parasites (excluding the bacteria and viruses), their habitat specificity within the host, frequency distribution, and also the occurrence of any interactions between different parasite populations.

An important reason for our lack of knowledge about the smooth flounder is the complexity of its estuarine habitat. The extreme variability of physical factors such as temperature and salinity leads to a diversity of habitats in close proximity, and often without clear boundaries. This situation leads to problems in sampling and field observation. It is ironic that such factors, which render an estuary difficult to study by conventional methods, actually facilitate the application of parasitological data.

An example will help to clarify this point. A fish, like any animal in nature, acts as a "biotic sampler" of its environment, and its parasite fauna comes to reflect this environment. The array of parasites capable of completing their life cycles in a particular habitat can thus be used to characterize it. In addition to obvious differences

in numbers and species of parasites present, it is also possible to characterize the parasites of a fish population by means of indices of diversity (Davis and Huffman, 1975). This procedure has the added advantage that the indices provide an estimate of the diversity of the free-living community, and community diversity has been used to detect and evaluate pollution (Wilhn, 1967; Wilhn and Dorris, 1968). Such an application of parasitological data is as yet in its infancy, but could be of value as a simple measure of environmental quality.

A parasite fauna can be used not only to characterize a particular environment, but to reflect host movements through different habitats. This principle has been used to "tag" the long range migrations of anadromous fishes (Margolis, 1963, 1965; Konovalov and Konovalova, 1969; Pippy, 1969), and more recently to study local movements (Olson and Pratt, 1973). By comparing smooth flounder parasite data from different areas of the estuary, it is possible to gain some knowledge of the movements and mixing of fishes from the different areas.

Due to the emphasis placed in this study on both the numbers and positions of parasites, it is imperative that accurate determinations of these factors be made. There is evidence, however, that changes in both factors occur when fish are maintained in the laboratory (MacKenzie and Gibson, 1970; Möller, 1976). In order to investigate these changes, and ensure that they do not affect the accuracy of the field data, it was decided to systematically sample smooth flounder which had been kept in the laboratory for up to four days.

I have mentioned that both ecological and evolutionary factors are involved in the formation of a parasite fauna. The major portion of this dissertation is concerned with ecological questions. During field

collections, however, winter flounder (Pseudopleuronectes americanus) were frequently collected incidentally. This species is very similar to smooth flounder, both in morphology and in diet. It is interesting, therefore, to compare their parasite faunas. Since their ecological opportunities for contact with parasites are very similar, and both species are opportunistic feeders, any marked differences could be ascribed to evolutionary factors.

There are several rather distinct sections comprising this study. The main body of the dissertation will be divided into five essentially self-sufficient units, each with a detailed introduction, methods, results, and conclusions. In addition to this general introduction, there will be a final discussion and summary.

The five divisions of the dissertation are as follows:

1. The parasites of smooth flounder - consisting of a compilation of all species found in or on this host, their taxonomic status, and notes on their general biology.
2. Parasite population dynamics - the seasonal fluctuations in prevalence and intensity) of all parasite species. Also considered will be site preferences of the parasites, including any changes resulting from different intensities of infection or levels of maturity, parasite frequency distributions, and a consideration of possible interspecific interactions.
3. The effect of laboratory holding time on a parasite fauna - a quantitative look at any changes in numbers and positions of parasites as their hosts are kept in the laboratory for up to four days prior to examination.

4. Intra-specific differences in parasite fauna - a comparison of smooth flounder parasites from hosts collected at two different sites within the estuary, and a consideration of how the sites might be characterized by these parasites.
5. Inter-specific differences in parasite fauna - to evaluate the importance of evolutionary factors when the ecological opportunities for parasite contact are very similar; a consideration of host specificity.

The Host

Smooth Flounder (Liopsetta putnami (Gill), 1864)

Other names: Smoothback flounder; Eelback; Foolfish; Christmas flounder; Plaice (Bigelow and Schroeder, 1953).

The smooth flounder is an artic-boreal species, distributed along the Western Atlantic coast from Labrador to Massachusetts Bay. It is a strictly inshore fish, inhabiting mainly estuaries, river mouths, sheltered bays, and harbors (Bigelow and Schroeder, 1953). The first report of smooth flounder from the Great Bay estuary, New Hampshire, was by Jackson (1922). The Great Bay estuary is near the southern limit of Liopsetta's geographic range. There is no evidence that smooth flounder extend to seaward beyond the inner reaches of Portsmouth Harbor.

There have been few studies of the biology of smooth flounder. Leim and Scott (1966) and especially Bigelow and Schroeder (1953) provide short summaries of known information. The only work dealing exclusively with smooth flounder is that of Laszlo (1972), who studied the Great Bay stock. The mariculture potential of smooth flounder is currently being explored (Sawyer, 1977, pers. comm.).

The smooth flounder is a small-mouthed species and its diet reflects this circumstance. Laszlo (1972) reported that the diet in Great Bay, New Hampshire consisted almost entirely of invertebrates; young fish (< 10 cm) preyed most heavily on molluscs (both bivalves and gastropods), but older (> 10 cm) animals consumed primarily annelids. Laszlo did not record specifically where he collected the flounder used in his food study, an omission that presents a problem because experience has shown that smooth flounder are opportunistic feeders whose prey tends to reflect their environment. Thus animals from different parts of the

bay often have different diets. Individual flounder from the same habitat also tend to exhibit differences in food preferences. These types of differences preclude most generalizations concerning the diet of individual fish.

While the list of food items given by Laszlo is quite comprehensive, the present study necessitates two additions. The first is the presence, especially in the lower estuary, of spionid polychaetes of the genus Polydora. These worms are the single most important food item for many young flounder.

The second addition is the calanoid copepod Eurytemora affinis, which reaches very high population densities in the upper estuary during the late spring (April and May) (Phillips, 1976). At this time it is the most abundant zooplanktor. It is also the most abundant food item, both in numbers and in volume, of smooth flounders of the two youngest age groups. No dietary information is available for older fish, but the larger animals would be less likely to be planktivorous. Eurytemora declines drastically in abundance during the summer months, and no other planktor achieves comparable densities. Flounder gut content analyses at these times show a return to the more typical mollusc-annelid diet.

The smooth flounder spawns during the early winter (Bigelow and Schroeder, 1953; Leim and Scott, 1966; Laszlo, 1972). It is not known whether the fish migrate to any extent within the bay in order to spawn. Smooth flounder are remarkable in that many of the males attain sexual maturity during their first year of life. The females mature at the age of two to three years.

There is no information available concerning fecundity of smooth flounder. Laszlo (1972) reported that the ripe eggs are over 1 mm in

diameter. This is slightly greater than winter flounder ova. The eggs of smooth flounder sink to the bottom but are not sticky like those of winter flounder (Laszlo, 1972; Sawyer, 1977, pers. comm.) Eggs fertilized in the laboratory and kept at near ambient outdoor water temperature (~0°C) hatched in from 21 to 45 days. Metamorphosis occurred a minimum of 51 days after hatching (Hoornbeek, 1977, pers. comm.) This period of planktonic existence is quite short in comparison to many other flatfish. It is possible to collect just metamorphosed juveniles (~1.3 cm) in the field in early May. These animals will have attained an average total length of over 8 cm by their first birthday.

There is no commercial fishery for smooth flounder, due primarily to its small size (max. 12 inches) and relatively limited distribution. Bigelow and Schroeder (1953), however, have stated that this fish "has been found so often in various markets among the winter flounder as to suggest that it is more plentiful along the coasts of northern New England, than is realized, generally."

PART II

Parasites of Smooth Flounder

Introduction

The majority of references to the parasites of smooth flounder simply record their presence with little mention of prevalence, intensity, or other biological factors. Those parasites that have been recorded from smooth flounder are listed in Table 1. Of these, the protozoans Cryptobia sp. and Cryptobia bullocki are the same animal, first reported by Bullock (1953) and ultimately described by Strout (1965). Among the trematodes, the only taxonomic problem is presented by Lepocreadium trullaforme. The status of this species is uncertain since Linton (1940) apparently identified "at least two different species as L. trullaforme" (Stunkard, 1969). The species was redescribed by Sogandares-Bernal and Hutton (1960) and certain specimens were identified as a new species, L. caballeroi. Stunkard (1969) considered some of Linton's material to represent another Lepocreadium species, L. areolatum (Linton, 1901) Stunkard, 1969. In 1972, he stated that almost all available specimens identified as L. trullaforme by Linton, including the specimen redescribed by Sogandares-Bernal and Hutton (1960), were actually L. areolatum. The only exception was some specimens from kingfish, Menticirrhus saxatilis, which he identified as L. setiferoides. As a result of this taxonomic chaos, the exact identity of the Lepocreadium species reported by Linton from smooth flounder is not known.

The nematode species reported by Ronald (1963) also require clarification. Ronald reported Terranova (=Porrocaecum-Phocanema) sp. larvae from several species of flatfishes. The only known species of

TABLE 1

Parasites Reported From Smooth Flounder (*Liopsetta putnami*)

Parasite	Reference
Protozoa	
Cryptobia sp.	Bullock, 1953; Strout, 1962
Cryptobia bullocki	Strout, 1965
Trematoda	
Homalometron pallidum	Linton, 1940
Lepocreadium trullaforme	Linton, 1940
Stephanostomum baccatum	Wolfgang, 1955; Ronald, 1960
Steringophorus furciger	Ronald, 1960
Podocotyle atomon	Ronald, 1960
Hemiurus communis	Ronald, 1960
Derogenes varicus	Ronald, 1960
Cryptocotyle lingua	Ronald, 1960
Cestoda	
Bothriocephalus scorpii	Ronald, 1958
Nematoda	
Terranova sp.	Ronald, 1963
stomachinae larvae	Ronald, 1963
Acanthocephala	
Echinorhynchus gadi	Ronald, 1963
Crustacea	
Argulus megalops spinosus	Wilson, 1944

this genus from the Canadian Atlantic is the codworm, T. decipiens, which matures in the harbor seal (Phoca vitullina). Ronald did not make a specific designation because he did not feel that it had been proven that Atlantic flatfish harbored only one species of this nematode. While this conservatism is commendable, there is no evidence that the specimens are any but T. decipiens.

Nematode larvae which could not be assigned to a genus were referred to by Ronald as "stomachinae larvae", considered to be early developmental stages of both Terranova and Contracaecum. Since the only identifiable larvae found in smooth flounder belonged to the former genus, it seems very likely that the younger forms also are Terranova decipiens.

There is a minor problem with Ronald's (1958) paper reporting the cestode Bothriocephalus scorpii from smooth flounder. On page 433, where he mentions the "location" of the parasite in a particular host, the scientific names of the sand flounder (Scophthalmus aquosus) and smooth flounder (Liopsetta putnami) are reversed. That it is the scientific names which were confused is evidenced by the ensuing explanatory paragraph, referring to the "twisted and knotted cestodes" blocking the caecal arms of sand flounder; S. aquosus has long pyloric caeca which could indeed be so blocked. Smooth flounder, however, have very short, broad caeca which amount to little more than bumps at the gastro-intestinal junction. There are no caeca to be blocked. It is necessary to acknowledge this error since the reported prevalence and intensity of B. scorpii are quite different in sand and smooth flounder.

It is apparent that the papers by Ronald (1958; 1960; 1963) comprise the most extensive treatment of smooth flounder parasites. These papers were based on fish collected at various sites in the Gulf

of St. Lawrence and in Nova Scotian waters. It is unfortunate, however, that little precise data are available concerning where the flounder were collected. By all accounts this is a fish found most commonly in brackish water. There are, however, several parasite species, notably S. baccatum and S. furciger, which are not known to be estuarine species. The parasite species reported by Ronald seem generally to reflect a more marine assemblage. If collected in an estuary, the flounder examined by Ronald could have acquired these parasites during a seaward migration. Alternatively, it may be that Gulf of St. Lawrence smooth flounder inhabit more oceanic areas than their southern relatives. A close examination of the flounder parasites from the Great Bay estuary, New Hampshire could provide information concerning this point.

For this reason, and to extend our limited knowledge of smooth flounder parasites, I decided to investigate these animals in the Great Bay estuary, New Hampshire.

Materials and Methods

Between June, 1974 and December, 1976, I collected 562 smooth flounder in all months of the year from the Great Bay estuary, New Hampshire (Figure 1). Collections were primarily with a beach seine, in winter by hook and line, and once with an otter trawl. Collection sites are indicated in Figure 1. The two primary collecting locations were near the mouth of the Lamprey River (Newmarket, New Hampshire) and in Trichy's Cover, adjacent to the General Sullivan Bridge (Newington, New Hampshire). The flounder were brought to the laboratory in aerated buckets and examined externally and internally for parasites. All protozoan and metazoan species were noted. Parasites were examined alive, and whole

mounts were made of representative helminths. Nematodes were fixed in hot 70% ethyl alcohol, cleared in glycerin-alcohol, and mounted in glycerin jelly. All other helminths were fixed in Demke's AFA, stained according to Lynch's precipitated borax-carmine method (Galigher and Kozloff, 1971), and mounted in Canada Balsam.

Results

Twenty seven species of parasites were discovered from smooth flounder. Of these, 24 are new host records. The parasites are listed in Table 2.

Discussion

Of the above 27 species, 10 occurred in less than 1% of the fishes and could be considered as incidental parasites. The ciliate genera Trichodina and Apiosoma belong in this category, as do the monogeneans Gyrodactylus sp. and the unknown immature form. These are all ectoparasitic species. For some of them, especially Gyrodactylus sp., the possibility exists that smooth flounder were infected artificially in the bag end of the collecting seine. Gyrodactylus is a common parasite of Fundulus heteroclitus, which were often captured along with Liopsetta. The opposite possibility was suggested by Strout (1962) with regard to the leech (Atlanticobdella bursata), which reportedly drops off during capture. That this leech may be more abundant than it appears is indicated by the abundance of Cryptobia bullocki, a hemoflagellate for which the leech is implicated as a vector (Strout, 1962). The leech referred to as Atlanticobdella has never been formally described. The name was applied by Raj (1962) in a dissertation, but never published. It is used here for convenience only.

TABLE 2

Parasites of Smooth Flounder from New Hampshire

Protozoa

Cryptobia bullocki
Trichodina sp.
Apiosoma sp.
Glugea stephani
Myxobilatus sp.
unidentified sporozoan 1
unidentified sporozoan 2

Monogenea

Protancyrocephaloides liopsettae
Gyrodactylus sp.
unidentified monogenean (immature)

Digenea

Lepocreadium setiferoides
Homalometron pallidum
Zoogonus lasius
Stephanostomum tenue
Cryptocotyle lingua
Opecoeloides vitellosus
Lecithaster confusus
Gynaecotyla adunca
Tubulovesicula pinquis

Cestoda

Proteocephalid (immature)

Nematoda

Spirurida (immature)
Ascarophis sp.

Acanthocephala

Pomphorhynchus rocci

Crustacea

Argulus laticauda
Ergasilus manicatus

Miscellaneous

glochidia (Mollusca: Unionidae)
Atlanticobdella bursata
(Annelida: Hirudinea)

Ascarophis sp., G. adunca, T. pinquis, and P. rocci are endohelminths, and all occur commonly in host species other than Liopsetta. Ascarophis sp. is a nematode, found quite commonly in winter flounder (Pseudopleuronectes americanus), but rarely in smooth flounder. The trematodes G. adunca and T. pinquis are parasites of shorebirds and silversides (Menidia menidia), respectively. According to Rankin (1940), G. adunca (=G. nassicola) uses the amphipod Talorchestia longicornis as a second intermediate host. This avian trematode can survive but not mature in smooth flounder. T. pinquis is a hemiurid species found locally in the body cavity of silversides and sticklebacks. Although one mature specimen (of three) was discovered in a similar location in flounder, their extreme scarcity precludes the possibility that Liopsetta is a normal definitive host.

The acanthocephalan Pomphorhynchus rocci utilizes the amphipod Gammarus tigrinus as a first intermediate host and matures in striped bass (Morone saxatilis), white perch (Morone americana), yellow perch (Perca flavescens), and large mouth bass (Micropterus salmoides), (Johnson and Harkema, 1971). These authors also recorded an extensive list of fishes from which juveniles and degenerate-encysted forms were recovered. Included in this list was an "unknown species of flounder". Encysted forms such as the above were found in a small number of smooth flounder. It is not known whether these flounder could serve as paratenic hosts.

The final "incidental" parasites are glochidia, larval molluscs of the Unionidae (fresh water mussels). The presence of parasites such as these gives an indication of the extreme euryhaline nature of smooth flounder.

The remaining 17 species are not all common parasites of smooth flounder. Indeed, the least common among them occur little more frequently than some of the "incidental" parasites. These species however share the characteristic of predictability, meaning that a year round sample of smooth flounder parasites from the estuary will predictably contain representatives of all 17. Year round sampling is necessary since most of these species vary seasonally in occurrence. Such seasonal fluctuations in parasitism are considered in subsequent sections of this dissertation.

The most common protozoan parasites of smooth flounder are the hemoflagellate Cryptobia bullocki and the microsporidan Glugea stephani. The life cycle of C. bullocki and its presumed leech vector has been mentioned.

The life cycle of Glugea is controversial, with disagreement centering on the necessity for an intermediate host. Recently McVicar (1975) and Olson (1976) have independently demonstrated that the cycle can run both ways, i.e. directly, and with a crustacean intermediate. Both workers found, however, that the presence of an intermediate resulted in higher intensity infections. The identity of any such intermediate in Great Bay is not known. The diet of smooth flounder includes numerous crustacea (copepods, amphipods) and presumably one or more could serve to transmit the Glugea infection.

The final three protozoan species found in smooth flounder are the myxosporidan Myxobilatus sp. and two unknown sporozoans. Positive identification of these latter species is not possible because neither apparently undergoes sexual reproduction in the flounder, and the sexual stages are essential to identify such forms. The two species are easily

separable however, since their appearance is quite different and they tend to occur at different times of year.

The first unknown sporozoan species is known only from the sporozoite (merozoite) stage seen frequently in scrapings from the intestine (Fig. 2). An organism of this appearance could belong to almost any sporozoan group. No other stage of the life cycle has been seen, and no pathology is apparent.

The second unknown sporozoan is more intriguing. The parasite is common in the late winter and spring and can reach high densities (Figure 3). Its appearance is suggestive of the asexual reproductive stages of the coccidian Eimeria anguillae, Leger and Hollande, 1922, an unusual species in that its asexual stages are extracellular. It is only after fertilization of the macrogamete that the zygote becomes intracellular, and there is no suggestion of this in smooth flounder. Eimeria anguillae was identified from eels (Anguilla rostrata) in the Great Bay estuary (W. L. Bullock, pers. comm.) It is possible that E. anguillae from these eels might infect the flounder, but not be able to complete sexual reproduction in the unnatural host. Asexual stages similar to those found in smooth flounder have also been found in Great Bay in killifish (Fundulus heteroclitus) and sticklebacks.

Myxobilatus sp. is found in the urinary bladder of smooth flounder. This species occurs both in smooth and winter flounder, and is considerably more common in the latter species. There is no apparent pathology associated with Myxobilatus infection.

One monogenetic and seven digenetic trematodes are found routinely in smooth flounder from the Great Bay estuary. The monogenetic trematode is a new genus of the Ancyrocephalinae, Protancyrocephaloides liopsettae

Burn, 1978. The animal is apparently specific for smooth flounder and has some unique biological features. These features will be dealt with in a subsequent portion of this dissertation.

The digenetic trematodes dominate the parasite fauna of smooth flounder, not only in numbers of species but also in numbers of individuals. Although the species present vary from season to season, they are always the most abundant group. This situation is due in part to the diversity and abundance of the digenes themselves, although seven species is not an overwhelming total. It is also due to the relative scarcity in the Great Bay estuary flounder of every other helminth group.

Of the seven digene species, two are found as metacercariae and five as adults. The two metacercariae are Cryptocotyle lingua and Stephanostomum tenue. C. lingua matures primarily in sea gulls, and its first intermediate host can be either Littorina littorea or Littorina obtusata. C. lingua cercariae encyst in the integument and especially in the fins of many fish and lead to the formation of conspicuous black spots.

The first intermediate host for S. tenue is Nassarius obsoletus (Martin, 1939). The cercariae encyst in or near the pericardial cavity of smooth flounder and several other fish, generally in very low numbers. S. tenue matures in the striped bass (Morone saxatilis).

The most common of the adult digenes in smooth flounder is Lepocreadium setiferoides. The life cycle of this worm was investigated by Martin (1938), who found the first intermediate host to be the mud snail, Nassarius obsoletus. Cercaria shed from this snail are not especially specific for a second intermediate host, having been found experimentally to infect a coelenterate, several turbellaria, and small polychaetes (especially spionids) (Martin, 1938; Stunkard, 1972).

Magendantz (1969) reported that the spionid Polydora ligni is heavily infected in nature in New Hampshire. This polychaete is a common food item for smooth flounder.

It is interesting that while L. setiferoides reaches densities of hundreds per fish in L. putnami, a very small percentage of these worms reach sexual maturity and produce eggs. This phenomenon was also noted by Magendantz (1969). It is probable that smooth flounder are not the most suitable definitive host for Lepocreadium.

L. setiferoides undergoes marked seasonal changes in abundance, but it is present in flounder throughout the year. The only other trematode for which this is true is Zoogonus lasius, which, however, is generally present at much lower densities than Lepocreadium. Like L. setiferoides, it uses the mud snail (N. obsoletus) as a first intermediate host. Stunkard (1938) infected several polychaetes and a turbellarian with Zoogonus cercearia from Nassarius. The preferred second intermediate host was Nereis virens, in which the worms encysted in the parapodia.

Homalometron pallidum is the largest of the digenes present in L. putnami, reaching lengths of up to 3 mm. It is abundant only during the summer months. According to Stunkard (1964), this trematode utilizes Hydrobia minuta as a first intermediate, and the cercaria may encyst in Hydrobia or in the bivalve Gemma gemma. Certain small polychaetes were also used as second intermediates.

Of the predictable digene parasites of smooth flounder, Opecoeloides vitellosus and Lecithaster confusus are the least conspicuous. O. vitellosus is never common, but is found in low numbers in spring and summer, and rarely at other times. The life cycle was investigated by Hunninen and Cable (1941). It includes the snail Mitrella lunata and the amphipods

Gammarus mucronatus and Amphithoe longimana. The first two species at least are known from the Great Bay estuary, and Laszlo (1972) found G. mucronatus in the gut of smooth flounder.

Lecithaster confusus occurs only in the spring, its presence corresponding to the period when flounder are feeding heavily on copepods. Hunninen and Cable (1943) reported that the life cycle of Lecithaster includes the snail Odostomia trifida and the copepod Acartia tonsa. Although this particular copepod has not been found in the stomach of smooth flounder, it is known to be present in the estuary (Croker, 1972). It is also possible that Lecithaster could run its life cycle through another calanoid such as Eurytemora affinis, a very common food item.

The only cestodes found in smooth flounder were immature proteocephalids found intermittently in the spring. These worms never showed any sign of strobilization and were probably transient inhabitants of the flounder gut. The intermediate host for a proteocepholid cestode would probably be one of the copepods that predominate the flounder diet at this time. Although exact identification of the immature cestode is not possible, it is probably Proteocephalus macrocephalus. P. macrocephalus is found in eels in the estuary during late spring.

Only one nematode species was found commonly in smooth flounder. These animals were small (< 2 mm) larvae of the Order Spirurida. The nematodes occurred both free in the intestine and encysted in the liver and mesenteries. It is likely that they infected the flounder by means of an arthropod (probably a copepod) intermediate host.

There were two species of Crustacea which parasitized Liopsetta in Great Bay, but neither occurred commonly. Both the copepod Ergasilus manicatus and the branchiuran Argulus laticauda have direct life cycles,

and infect their final host as planktonic larval stages. Both are also relatively non host-specific, having been reported from numerous marine and estuarine fish species. A. laticauda is common on eels (W. L. Bullock, pers. comm.) and E. manicatus is seen frequently on sticklebacks and silversides (Menidia menidia). This species has also been reported from Fundulus heteroclitus (Roberts, 1970).

In comparison to the works of Ronald (1958; 1960; 1963), the parasites of smooth flounder from New Hampshire show a distinctly more estuarine orientation, with all parasites characteristic of brackish water. This is in keeping with what we know of their local life history. Ronald, however, reported several species (i.e. Stephanostomum baccatum, Steringophorus furciger, Bothriocephalus scorpii) which are not found in estuaries. These parasites provide evidence that smooth flounder from the Gulf of St. Lawrence are less restricted to estuaries than are their more southern relatives.

There is little evidence for pathogenicity for most of the parasites of smooth flounder. The internal helminths are not implicated, and noectoparasite is common enough to elicit any pronounced host response (i.e. excessive mucus, inflammation, etc.) A parasite whose pathogenicity has been well studied is C. lingua. Sindermann and Rosenfield (1954) demonstrated that massive cercarial infections could blind and kill immature herring. More recently, McQueen et al (1973) studied the inflammatory response of plaice to Cryptocotyle infection. Although they found the reaction to be remarkably limited, there was serious muscle damage to 0+ age group animals. In younger fishes, the cercaria sometimes penetrated beyond the dermis into the muscles. The actual muscle damage was apparently the result of secondary bacterial infection.

McQueen and his co-workers believed that high intensity infections could be lethal for small plaice. There is no indication that such high intensity infections occur in smooth flounder, and no cercarial muscle penetration has been observed. In contrast, young winter flounder have been observed with C. lingua infections in the muscles and viscera.

The only parasite believed to seriously affect smooth flounder is the microsporidan, Glugea stephani. Glugea cysts occur most frequently in the wall of the intestine, causing hardening and thickening. In heavy infections the intestine may be nearly occluded and its epithelium sloughed off. Stunkard and Lux (1965) studied the effect of age, sex, diet, season, and geographic location on the occurrence of the disease in winter flounder. They found that up to 20% of age group 0 flounder were heavily infected, and were of the opinion that these fish did not survive into their second year.

Glugea stephani infections in smooth flounder are not as prevalent or intense as those of winter flounder. Heavy infections do occur, however, and in these the probability of death is high. As in winter flounder, Glugea infections do not seem to have much effect on older age groups.

PART III

Aspects of the Population Biology of Smooth Flounder Parasites

Introduction

The study of parasite populations is complicated by the difficulty of defining a "population" of many parasitic species. The general definition of a population is a group of interbreeding organisms of the same species that occupies a particular space. Unfortunately this definition is ambiguous when applied to parasites. The question, as stated by Esch, Gibbons and Bourque (1975) is whether "all members of a given parasite species within a single host constitute a population, or should all members of a species in all hosts within a given ecosystem be considered a population?" To circumvent the problem, Esch et al suggested that the former grouping be referred to as an infrapopulation, and the latter as a suprapopulation. The present investigation deals exclusively with the parasite infrapopulations found in smooth flounder. My primary areas of interest were the seasonal and maturation cycles exhibited by many parasites, their habitat specificity, interspecific interactions, and frequency distributions.

Seasonal changes in abundance and maturation have been observed for many fish parasite infrapopulations (Kennedy, 1977). Such cycles have been reported for monogeneans (Paling, 1965; Davies, 1967; Rawson, 1976), digeneans (Wooten, 1973), cestodes (Kennedy and Hine, 1969), acanthocephalans (Muzzall and Rabalais, 1975) copepods (Boxshall, 1974), nematodes (MacKenzie and Gibson, 1970), leeches (Halvorsen, 1971), and protozoa (Noble, 1957; Kabata, 1963). Kennedy (1970, 1975) stressed the importance of distinguishing between abundance and maturation cycles,

since there is no consistent correlation between the two. He concluded that most seasonal cycles can be correlated to changes in fish behavior and diet, and directly or indirectly to physical changes in the water, especially its temperature.

Kennedy (1975) stated that maturation cycles were correlated frequently with temperature, but that other factors (including host maturation) might play a role. There is an obvious connection between parasite maturation and recruitment of the next generation. Thus, although the factors influencing maturation and abundance cycles may be different, the cycles can be interdependent.

The only investigations concerned with maturation and/or seasonal abundance cycles in smooth flounder are those of Strout (1962) and Magendantz (1969). Strout found no seasonal change in the occurrence of the blood flagellate, Cryptobia bullocki. Magendantz reported a high incidence of the trematode Lepocreadium setiferoides in late spring and summer, gradually decreasing until mid winter. Mature worms were found in spring and late autumn. No other species of parasite have been investigated in smooth flounder.

Parasites are found characteristically in certain sites within their host. This site specificity may be not only for a particular organ, but for a specific part of that organ. This is especially true in the alimentary canal, which can be subdivided considerably. The situation in the gut may also be complicated by ontogenic and circadian migrations of the parasties (Croll, 1976), and site segregation as a result of interspecific competition (MacKenzie and Gibson, 1970; Holmes, 1971, 1973).

In recent years, Ulmer (1971), Holmes (1973) and Cromptom (1973) have reviewed the phenomenon of site specificity. These workers, as well

as Read (1971), have tended to assume a relative homeostasis within the regions of the gut of a host, and thus described the enteric distributions of certain parasites in terms of "preference" for a particular gut site. Croll (1976) argued that in many cases the situation is more dynamic, involving changes in the physiochemical conditions in a certain area. In particular he showed that the nematode, Nippostrongylus brasiliensis seems to be dispersed in the rat intestine according to the presence of food in the lumen. Croll proposed the term "habitat" to suggest a causal relationship between the parasite and its surroundings. On the other hand, Croll emphasized that in many instances, especially outside of the gut, distributions of parasites previously ascribed to site selection could be explained as easily by reference to the "plumbing" of the host in conjunction with reduced parasite survival in less than optimal areas.

Little information is available concerning habitat specificity of the parasites of Liopsetta putnami. Magendantz (1969) reported that Lepocreadium setiferoides were found in the anterior intestine. There has been no systematic study of this trematode or any other smooth flounder parasite, involving either the spatial distribution of parasites or the factors which contribute to it.

Interactions between species of fish parasites have been reported on numerous occasions. Most of the characteristic interactions of free living organisms can also occur between parasite species; however, Kennedy (1975) stated that "the effect of one parasite population upon another is more often spasmodic, fortuitous, and unpredictable." Positive or negative associations have been described between two or more species of fish parasites by Noble (1961); Noble, King, and Jacobs (1963); and Thomas (1964). Interactions may also include competitive exclusion, niche

diversification, and site segregation (Chappell, 1969b; MacKenzie and Gibson, 1970; Holmes, 1971; 1973). The mechanisms for most of these interactions have not been demonstrated, nor has there been any investigation of such interactions among the parasites of smooth flounder.

The study of frequency distributions of parasites in or on their host has been neglected until relatively recently (Williams, 1961). This is unfortunate since these distributions can provide information concerning both the parasite and its effect on the host. Although fish parasites may be randomly distributed (Hopkins, 1959; Valentine and Phelps, 1977) more commonly they are found in so-called "overdispersed" or "contagious" distributions (i.e. those in which the variance exceeds the mean) (Kennedy, 1968; Kennedy and Hine, 1969). Overdispersed distributions can frequently be fitted to, and thus described by specific mathematical functions. Some of the theoretical distributions which have been fitted are the logarithmic series, Neyman A, and the negative binomial (Williams, 1964; Kennedy, 1970, 1975). The negative binomial has been fitted to the frequency distribution of several fish parasites (Pennycuick, 1971b; Anderson, 1974; MacKenzie and Liversidge, 1975), and has been used as a fundamental model and to indicate parasite induced mortality (Crofton, 1971a; Lester, 1976). The frequency distributions of smooth flounder parasites have never been investigated.

As a result of the minimal knowledge of the biology of smooth flounder parasite infrapopulations, I decided to investigate seasonal and maturation cycles, habitat specificity, frequency distributions, and any associations between parasite species in the Great Bay estuary, New Hampshire.

Materials and Methods

Between May, 1975, and December, 1976, 192 smooth flounder (Liopsetta putnami) of the 1975 and 1976 year classes were collected by beach seine from the Lamprey River near its junction with the Great Bay in Newmarket, New Hampshire (Fig. 1). Collections were made at least once per month except during December, 1975 and January and February 1976, when ice prevented sampling. At these times a limited number of older fish were collected by hook and line. Water temperature and salinity were recorded at the time of all collections. All fish were brought to the laboratory and necropsied within 36 hours of capture. The total length and sex of the flounder were recorded. All protozoan and metazoan parasites were identified and counted. The location and state of maturity of all parasites was noted. The alimentary canal was divided into five regions (stomach, 3 equal portions of intestine, rectum) to more accurately locate the habitats of different enteric species.

Frequency histograms of parasites per fish were plotted for all metazoan species, and where numbers permitted, I attempted to fit these distributions to the negative binomial (Bliss and Fisher, 1953; Crofton, 1971b) or the log series (Williams, 1964). Because of the non-normality of the frequency curves, differences in intensity of infection between months were tested by the non parametric Kruskal-Wallis test. Individual comparisons between months were made by a non-parametric multiple range test as suggested by Zar (1974). Differences in prevalence between months were tested by 2 X 2 contingency tables and subsequent chi-square analysis. For the analysis of habitat specificity within the gut, the mean intensity and percentage of the total infection were calculated for each section for each parasite species. The 1975 and 1976 year classes were examined jointly,

and monthly means were calculated to discover any change in habitat over time. The 0 and 1 age-group fish collected simultaneously were examined for any age differences. Also, the monthly samples of the more common metazoans, (Lepocreadium setiferoides, H. pallidun, Z. lasius,) were grouped and ranked in order of intensity of infection and subgroups examined for any change in distribution with increased crowding. Coefficients of variation were calculated for all such groups. All statistical tests of significance were made at the 5% level.

The point of attachment to the gills of the monogenean Protancyrocephaloides liopsettae was recorded with regard to three locations. These were:

1. The side of the buccal cavity (left or right).
2. The gill arch (numbered 1 to 4 from front to back).
3. The position on the arch (dorsal, medial, or ventral third).

The equality of the occurrence of monogenes on one side or the other of the buccal cavity was tested by a chi-square test.

Due to the non-normal distributions of most parasites, the possible associations between parasite species in each sample were examined by calculation of Spearman's rank correlation coefficient (Snedecor and Cochran, 1967).

Results

The water temperature and salinity of the Lamprey River during the study period are presented in Figs. 6 and 7.

Lepocreadium setiferoides

This was the most common parasite species of Liopsetta in the Lamprey River. Although it was found in the intestine and rectum during

all months of the year, its abundance varied markedly.

Seasonal Periodicity (Table 3)

In May, 1975, the intensity of infection with L. setiferoides in the newly metamorphosed flounder was very low and did not change significantly in June or July. Intensity increased significantly in August, and peaked in September and October. The November sample showed a significant decline. There are no samples of 1975 year class fish for the period December, 1975 to February, 1976. Older fish collected during this time, however, showed a low level of parasitism by Lepocreadium. The 1975 year class flounder collected in March, 1976, were infected lightly. It is likely that the winter occurrence of the trematode was low in the young fish. The decline in intensity from November to March was significant.

Lepocreadium in 1975 year class fish did not show any significant change in intensity between March and April, 1976, but did increase significantly in May. No 1975 year class fish were sampled in June and July; however, the August sample showed a significant increase in intensity. There was no change in September. The intensity of infection with Lepocreadium declined significantly in October, and this downward trend continued through December. It is apparent from these data that the annual pattern of Lepocreadium intensity in Liopsetta was similar for the first two years of the fish's life. Beginning with low levels of infection in the late spring, the infections gradually increased over the summer, peaked in early fall, then rapidly declined.

The annual prevalence pattern was not so clearly defined as that for intensity. This was due to the extreme abundance of Lepocreadium. For May, June and July of 1975, the prevalence values were significantly

TABLE 3

Monthly mean intensity (± S.D.) and prevalence of *Lepocreadium setiferoides* in 1975 and 1976 year class smooth flounder

	1975 year class			1976 year class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	1.4 ± 1.1	80	-	-	-
June	10	3.4 ± 5.2	60	-	-	-
July	10	0.9 ± 1.3	50	-	-	-
Aug.	10	40.7 ± 32.5	100	-	-	-
Sept.	10	205.5 ± 204.3	100	-	-	-
Oct.	10	134.1 ± 109.2	100	-	-	-
Nov.	10	46.3 ± 48.9	90	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0.6 ± 1.1	22.2	-	-	-
April	9	1.2 ± 2.0	44.4	-	-	-
May	7	3.0 ± 2.2	85.7	7	0	0
June	-	-	-	10	11.6 ± 9.1	100
July	-	-	-	10	99.2 ± 102.4	100
Aug.	5	432.4 ± 226.7	100	10	128.3 ± 50.2	100
Sept.	5	489.8 ± 327.1	100	10	138.6 ± 77.9	100
Oct.	6	84.3 ± 88.6	100	10	73.1 ± 104.1	100
Nov.	6	33 ± 30.7	100	10	35.1 ± 27.6	100
Dec.	5	8.4 ± 3.3	100	10	28.1 ± 66.8	70

lower than for the other samples. This corresponds to the pattern for intensity. For the months August through October, however, all fish sampled were infected by the trematode, and the decline in November was not significant. As a result of this profusion of trematodes, prevalence did not provide so clear a picture of seasonal abundance changes as did intensity.

The decrease in prevalence between November, 1975, and March, 1976, was significant and corresponds to the change in intensity for the same period. The increase between March and April was not significant, nor was that between April and May. In sum, however, the change between March and May was a significant one. No 1975 year class fish were collected in June or July, 1976, and from August to December the prevalence remained at 100%.

The initial acquisition of Lepocreadium by 1976 year class flounder was similar to the 1975 pattern. No trematodes were found in the May, 1976 sample; however, intensity increased significantly for every month between May and August. There was no change between August and September, and then intensity declined significantaly in October, November, and December.

The prevalence of L. setiferoides in 1976 year class fish showed only a rough approximation of the intensity pattern. The difference between May (0%) and June 100%) was significant, but the 100% prevalence of this species between June and November precluded any further differentiation. The decline to 70% in December corresponds to the change in intensity, but was itself not significant ($.1 > p > .05$).

The pattern of intensity was similar for the first two years of the fishes life. A more detailed comparison of the 1975 and 1976 year

classes for the months August through December, 1976, revealed a difference in the magnitude of the infections. The older fish showed a significantly greater intensity of infection for the months of August and September. These months coincide with the peak mean intensity for both age groups. There was no other difference in intensity, and no difference in prevalence between the two groups of fish.

While the patterns of initial acquisition of Lepocreadium were similar for both 1975 and 1976 flounder, there were differences between the years. Abundance increased more abruptly in 1976, although it never reached as high a mean intensity. For the 60 fish collected between June and November of each year, both prevalence and intensity were significantly greater in 1976.

The level of maturity of L. setiferoides in Liopsetta was never high. For the 1975 year class flounder, mature worms were found in only 4 of the 15 monthly samples. These months (and the percentage of mature worms) were: June 1975 (5.9%), September 1975 (0.1%), November 1975 (1.1%), and March 1976 (4.3%). In the 1976 year class, mature worms were found only in July, and at a level of only 0.1%. The pattern of maturation was not consistent for the two years. There was no difference in percent maturity between the age groups or year classes of flounder.

Habitat Specificity

Lepocreadium setiferoides was found characteristically in the intestine and rectum of the smooth flounder but not in the stomach (Table 4A, Fig. 8A). The mean percentages of L. setiferoides in the five gut sections of 1975 and 1976 year class flounder varied greatly between individuals. The amount of variability between the percentages in a particular section in different hosts can be quantified as a coefficient

TABLE 4

Mean Percentages of the total infection of different helminths in the gut sections of 0+ age group smooth flounder (1975-1976) (ST = stomach, I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, R = rectum)

		ST	I	II	III	R
A.	L. setiferoides	0	41.6	17.6	25.8	15.1
B.	H. pallidum	0	39.2	29.0	26.5	5.4
C.	Z. lasius	0	4.5	2.8	19.9	77.3
D.	O. vitellosus	0	18.4	5.3	32.5	43.8
E.	L. confusus	0	9.2	29.0	51.5	10.2
F.	Spirurid larva	0	60.7	33.0	5.7	0.6
Σx		0	173.6	116.7	161.9	152.4
$\bar{x}$		0	28.9	19.5	26.9	25.4

of variation (i.e. the standard deviation as a percentage of the mean). These coefficients also allowed a comparison of the relative variability in the different segments. The calculated coefficients of variation for the individual gut sections were: intestine 1 - 78.7%, intestine 2 - 79.1%, intestine 3 - 94.2%, and rectum - 135.7%. The variability is especially apparent in the rectum.

Since the distribution of parasites within the gut has in some cases been correlated with the distribution of food, and since the distribution of food in the gut of newly captured flounder varied greatly, I attempted to determine the relationship between these factors. The food in the fish gut passes out within 24 hours in the laboratory, so that if the distribution of parasites followed this stimulus, the variation between segments should be less at this time. The coefficients of variation between gut sections were calculated for host indiviudals posted on the day of capture, and for those held one day in the laboratory. The means of these coefficients were almost identical, despite the difference in food distribution.

The differences between the monthly mean percentages of total infection for each gut section of age group 0 flounder were considerable (Table 5). There was no consistent annual pattern to these changes, but the great variation within each sample, combined with the relatively small sample sizes, made recognition of any pattern difficult. There was a tendency for the trematodes to be concentrated in the anterior intestine in those months (e.g. May, 1975; June, 1975; June, 1976) with relatively low intensity infections. This tendency could be more fully examined when the host individuals were ranked in order of total intensity of Lepocreadium infection, and the mean percentages per section calculated

TABLE 5

Monthly Mean Percentages of the L. setiferoides Population in each gut section of 0+ age group Smooth Flounder. (I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, R = rectum)

1975	n	I	II	III	R
May	4	91.7	8.3	0	0
June	6	60	0	31.2	8.8
July	5	35	1.0	55	0
Aug.	10	79.7	9.5	10.1	0.7
Sept.	10	36	21.7	24.2	18.1
Oct.	10	25.2	18.6	36.3	20
Nov.	9	26.7	22.4	32	18.8
1976					
June	10	80.4	6.3	2.6	10.8
July	10	37.3	17.8	23.1	22.1
Aug.	10	51.5	17	22.9	8.8
Sept.	10	30.3	20.3	39.1	10.3
Oct.	10	36	24	25.7	14.3
Nov.	10	91	23.2	23.4	44.4
Dec.	7	33.5	31.5	27.9	7.2

Table 6, Fig. 9). The percentages were quite consistent at the different intensities, however the parasites were more evenly distributed in the higher density infections. Table 6 also includes the mean coefficient of variation calculated by averaging the coefficients from individual flounder within the abundance subgroups. The decline in this index at higher intensities further indicates that variation between the gut sections declined as trematode numbers increased.

The mean percentages of total infection for the 1975 year class flounder collected in August, September, October, November, and December, 1976 were: intestine 1 - 24.4%, intestine 2 - 27%, intestine 3 - 25.8%, and rectum - 12.8%. For 1976 year class fish collected during the same period the mean percentages were: intestine 1 - 32%, intestine 2 - 22.7%, intestine 3 - 27.8%, and rectum - 17.3%. The only difference was the slight decrease in trematodes in the anterior intestine and a similar increase in the posterior region in the 1975 class. This could be a result of the higher mean intensity of infection in the older fish.

Frequency Distribution

The coefficient of dispersion (variance ÷ mean) for the monthly samples of Lepocreadium was consistently far greater than unity, indicating a contagious (overdispersed) distribution. The monthly samples, however, were not large enough to provide a meaningful frequency histogram, and the seasonal abundance changes prevented combining these samples. The description of a specific frequency distribution for Lepocreadium was, therefore, not possible.

Homalometron pallidum

This trematode was found in the intestine and rectum of smooth

TABLE 6

Effect of Crowding on Habitat Specificity Mean Percentages and Coefficients of Variation of the L. setiferoides Population in Each Gut Seciton of 0+ Age Group Smooth Flounder. Data arranged in terms of Increasing Total Infection. (RA = range of parasites/fish, $\bar{x}$ = mean parasites/fish, m = total fish, I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, RC = rectum, C.V. = coefficient of variation).

RA	$\bar{x}$	n	I	II	III	RC	C.V.
1-5	2.7	20	46.8	12.5	25.8	15	169.9
5-20	11.6	20	44.8	18.1	19.8	17.3	126.3
20-51	37.1	20	44.9	16.2	23.2	15.7	108.3
56-86	69.5	20	42.8	19.6	21.5	16.2	89.4
87-153	110.7	20	35.2	17.4	33	14.4	80.5
187-588	283.4	17	33.9	22.3	32.5	11.4	81.6

flounder during late spring, summer, and early fall. H. pallidum is the largest of the enteric trematodes of Liopsetta in the Lamprey River.

Seasonal Periodicity (Table 7)

In May, 1975, the initial sample of 1975 year class fish were parasitized by Homalometron at a low intensity. This infection increased significantly in June and again in July. Even at its highest level, however, (July mean intensity = 3.4), it did not approach the density of Lepocreadium infections. H. pallidum intensity declined significantly in August, and the species remained at a low level until its complete disappearance in November. No Homalometron were found in any fish examined over the winter (December-February) months, nor in the more systematic surveys of 1975 year class fish in March and April, 1976. The trematode was present in May, but the increase from April was not a significant one. No 1975 year class flounder were sampled in June and July, 1976. In August, the trematodes were present, but at a low level. As in 1975, the trematodes remained at a low level through October, and disappeared in November. There was no statistically significant difference in intensity of Homalometron between any of the 1976 samples of 1975 year class fish.

The pattern of Homalometron prevalence for the 1975 year class fish was similar to that for intensity. Although the maximum prevalence (= 90%) for the July 1975 sample corresponded to the intensity peak, there was no significant change in prevalence over the first three months sampled (May - July). The decline in August was significant, and the downward trend continued. As in the case of intensity, however, there was no further statistically significant change until the trematode disappeared in November. There was no discernable pattern of prevalence for Homalometron in 1975 year class flounder collected in 1976. The parasites occurred in

TABLE 7

Monthly Mean Intensity (± S.D.) and Prevalence of *Homalometron pallidum* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0.8 ± .4	80	-	-	-
June	10	2.6 ± 3.5	70	-	-	-
July	10	3.4 ± 2.4	90	-	-	-
Aug.	10	0.6 ± 0.8	40	-	-	-
Sept.	10	0.5 ± 1.1	20	-	-	-
Oct.	10	0.2 ± 0.6	10	-	-	-
Nov.	10	0	0	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0	0	-	-	-
April	9	0	0	-	-	-
May	7	0.9 ± 1.2	42.9	7	0	0
June	-	-	-	10	0.5 ± 1.1	20
July	-	-	-	10	0.6 ± 1.0	30
Aug.	5	0.2 ± 0.4	20	10	0.4 ± 0.7	30
Sept.	5	0.6 ± 1.3	20	10	0.2 ± 0.4	20
Oct.	6	0.2 ± 0.4	16.7	10	0.3 ± 0.9	10
Nov.	6	0	0	10	0	0
Dec.	5	0	0	10	0	0

the same months (May through October) as in 1975.

Homalometron was not as common in 1976 as it had been in 1975. No trematodes were found in the May sample of 1976 year class fish. The parasites were present in Liopsetta from June through October, but always at low levels of prevalence and intensity. Unlike 1975, there were no significant fluctuations in abundance over the summer. Despite these differences, the months in which H. pallidum occurred were almost the same in age group 0 fish for 1975 and 1976.

The percentage of mature H. pallidum corresponded closely to its abundance cycle in 1975, being highest during the month (July) of highest abundance. However, some parasites were mature in every monthly sample except May, and there was no statistically significant difference in the percent maturity for the different months. The percentages of mature worms was high relative to Lepocreadium, ranging in 1975 from 38.5 to 73.5 percent of the worms found. Although the abundance of Homalometron was down in 1976, an average of 75% of them were mature.

In order to study any age related differences in the Homalometron carrying hosts, samples were made of 1975 and 1976 year class flounder during the period August through December, 1976. There were no statistically significant differences in the prevalence or intensity of H. pallidum between the two year classes.

Habitat Specificity

Like Lepocreadium, Homalometron was found characteristically in the intestine and rectum of Liopsetta (Table 4B, Fig. 8B). The trematode tended to occur more frequently in the proximal third of the intestine, and least frequently in the rectum. Like Lepocreadium, the percentages of the total found in a given gut section varied between individuals.

The relative amounts of variation, as reflected by the coefficients of variation calculated for each section were: intestine 1 - 109.3%, intestine 2 - 122.8%, intestine 3 - 140%, and rectum - 292.7%. These values are similar to those calculated for Lepocreadium, and in both species the rectum was the most variable section.

The monthly mean percentages of the total infection for each gut section for H. pallidum were variable, due probably to the small sample sizes and the great individual variability. When arranged according to intensity of infection, and divided into three equal sized groups, the mean percentages per section changed somewhat (Table 8). There was no clear pattern of change among the percentages, however the trematodes were distributed more evenly between segments at higher population densities. This tendency was also reflected in the decrease of the mean coefficients of variation in the higher density subgroups.

As a result of the low prevalence of Homalometron in fishes collected during the period of August through December, 1976, it was not possible to compare the habitat specificities of the trematodes in different year classes. There did not appear to be any dramatic difference in distribution between the different age hosts.

Frequency Distribution

The limited total number of infected fish, and the seasonal fluctuations in abundance, prevented the fitting of a frequency curve to the H. pallidum data. The variance to mean ratio was greater than one, indicating a contagious distribution.

Zoogonus lasius

Zoogonus was the only trematode aside from Lepocreadium found in the gut of smooth flounder year round in the Lamprey River. It occurred

TABLE 8

Effect of Crowding on Habitat Specificity. Mean Percentages and Coefficients of Variation of the H. pallidum Population in each Gut Section of 0+ Age Group Smooth Flounder. Data arranged in order of increasing total infection. (RA = range of parasites/fish, $\bar{x}$ = mean parasites/fish, n = total fish, I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, RC = rectum, C.V. = coefficient of variation).

RA	$\bar{x}$	n	I	II	III	RC	C.V.
1-2	1.1	11	45.5	27.3	27.3	27.3	200
2	2.0	11	40.9	36.4	36.4	13.6	161.6
3-11	4.8	12	31.7	16.7	16.7	31.8	119.9

in the intestine and rectum of its host.

Seasonal Periodicity (Table 9)

Despite its year round occurrence in smooth flounder, there was no significant seasonal fluctuations in prevalence or intensity. The relatively small monthly changes in abundance did not follow any consistent pattern. In addition, it was not possible to follow the maturation of Zoogonus since the thin walled egg was difficult to discern.

Although neither the 1975 nor 1976 year classes showed any seasonal fluctuations, there was a significantly greater number of worms present during 1975. In addition, there was a significant difference in intensity of infection between the age groups during the period August through December, 1976. The 1975 year class flounder were more heavily parasitized than the 1976 class. In neither of the above instances was there any significant difference in prevalence.

Habitat Specificity

Zoognous was found most frequently in the rectum and posterior intestine of Liopsetta (Table 4C, Fig. 8C). It was associated more closely with one section of gut (i.e. the rectum) than were Lepocreadium or Homalometron. In contrast to the other species, the coefficient of variation calculated for Zoogonus in the rectum was considerably lower than that for the other gut segments. The coefficients for the segments still exhibited great variation. They were: intestine 1 - 781.8%, intestine 2 - 503%, intestine 3 - 161.3%, and rectum - 44.8%. With the exception of the rectum, and to a lesser extent the distal third of the intestine, these coefficients of variation were considerably greater than those for Lepocreadium and Homalometron.

The monthly means of position percentages were not meaningful

TABLE 9

Monthly Mean Intensity (± S.D.) and Prevalence of *Zoogonus lasius* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0.4 ± 0.5	40	-	-	-
June	10	2.8 ± 4.6	70	-	-	-
July	10	0.6 ± 1.0	40	-	-	-
Aug.	10	2.2 ± 4.9	50	-	-	-
Sept.	10	1.1 ± 1.6	40	-	-	-
Oct.	10	5.8 ± 5.9	80	-	-	-
Nov.	10	2.4 ± 2.8	70	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0.2 ± 0.7	11.1	-	-	-
April	9	1.8 ± 1.8	66.7	-	-	-
May	7	0.7 ± 0.9	42.9	7	0.1 ± 0.4	14.3
June	-	-	-	10	0.7 ± 1.0	40
July	-	-	-	10	0.5 ± 0.7	40
Aug.	5	3.0 ± 3.5	60	10	1.2 ± 3.1	30
Sept.	5	10.4 ± 18.3	100	10	0.9 ± 1.3	40
Oct.	6	3.3 ± 3.5	50	10	0.5 ± 0.8	30
Nov.	6	1.0 ± 1.7	33.3	10	4.0 ± 11.3	40
Dec.	5	2.6 ± 5.8	20	10	0.2 ± 0.6	10

because of the small sample sizes and the great internal variation. When trematodes were arranged in order of intensity, and divided into three groups, the group mean percentages per segment, and the mean coefficients of variation between gut segments showed no discernable change in distribution, aside from a slight tendency for the parasites to spread anteriorly at higher intensities (Table 10). In conjunction with this tendency, the mean coefficient of variation between gut segments decreased as intensity increased.

There was no significant difference in the habitat specificity of Zoogonus in 0+ and 1+ age group flounder.

Frequency Distribution

Since the 0+ age group fish in both 1975 and 1976 showed no seasonal fluctuations in Zoogonus abundance, it was possible to combine the monthly samples and construct frequency histograms (Fig. 11). The data for 1975 were fitted successfully to the negative binomial (X^2 = 4.17, df = 7), when all expected frequencies less than one were combined. The estimate of k (measuring overdispersion) calculated for the 1975 data was 0.429. The 1976 data were fitted to a truncated negative binomial (X^2 = 2.21, df = 3) under the same circumstances. The truncation was of the one value (X = 36) in the histogram greater than 10. The estimated value of k was 0.381.

Opecoeloides vitellosus

O. vitellosus is a trematode found in the intestine and rectum of smooth flounder during the spring, summer, and early fall. Although found in all regions of the intestine, it occurred more commonly in the rectum.

TABLE 10

Effect of Crowding on Habitat Specificity. Mean Percentages and Coefficients of Variation of *Z. lasius* in each Gut Section of 0+ Age Group Smooth Flounder. Data arranged in order of increasing Total Infection. (RA = range of parasites/fish, $\bar{x}$ = mean parasites/fish, n = total fish, I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, RC = rectum, C.V. = coefficient of variation).

RA	$\bar{x}$	n	I	II	III	RC	C.V.
1	1	20	0	0	20	80	200
1-3	1.7	20	0	5	24.2	70.8	175.3
3-36	6.5	21	0.1	3.3	15.8	80.8	156.3

Seasonal Periodicity (Table 11)

The mean monthly intensity of Opecoeloides in 1975 was never high. The young fish sampled in May were not infected, and the worms present in June did not constitute a significant increase. The intensity did increase significantly in July, and maintained the same level of infection in August. Intensity declined significantly in September, and the worms disappeared in October. The sporadic samples of older fish during the winter months were uninfected. O. vitellosus were not detected again in 1975 year class fish until April, 1976, and then at a low level. The trematodes were present in the April, May, and August samples (none were taken in June and July), and then were not found again. At no time in 1976 did the monthly intensity of Opecoeloides in 1975 year class fish vary significantly.

The prevalence of Opecoeloides in 1975 closely followed the pattern set by intensity (Table 11). The percentage of infected fishes increases significantly in July, held steady through August, then declined in September. Although the species was found in three monthly samples of yearling fish in 1976, the prevalence never changed significantly.

The 1976 year class of flounder was parasitized by Opecoeloides in June and July only, and in neither month did the prevalence or intensity of the trematode depart significantly from zero.

The maturation pattern of O. vitellosus tended to follow the fluctuations in mean intensity. O. vitellosus were most common in 1975 during July and August, and the percentages of mature worms in these months were 42.9 and 77.8% respectively. The single trematode found in September was mature, however, this was not an adequate sample to make any conclusions. In 1976, mature worms were found in the yearling fish only in

TABLE 11

Month Mean Intensity (± S.D.) and Prevalence of

Opecoeloides vitellosus in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0	0	-	-	-
June	10	0.3 ± 0.7	20	-	-	-
July	10	0.7 ± 0.9	50	-	-	-
Aug.	10	0.9 ± 0.9	60	-	-	-
Sept.	10	0.1 ± 0.3	10	-	-	-
Oct.	10	0	0	-	-	-
Nov.	10	0	0	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0	0	-	-	-
April	9	0.1 ± 0.3	11.1	-	-	-
May	7	1.4 ± 3.4	28.6	7	0	0
June	-	-	-	10	0.3 ± 0.5	30
July	-	-	-	10	0.3 ± 0.7	20
Aug.	5	0.2 ± 0.4	20	10	0	0
Sept.	5	0	0	10	0	0
Oct.	6	0	0	10	0	0
Nov.	6	0	0	10	0	0
Dec.	5	0	0	10	0	0

August. The percentages of mature worms in the 1976 year class were 33 and 100 in June and July, respectively.

Although the initial acquisition of Opecoeloides was similar in 1975 and 1976 0+ age group fish for the first months, overall the trematodes were more abundant in 1975. Since there were no 1976 year class fish parasitized by O. vitellosus during the August through December period, it was not possible to directly compare these fish to the yearlings.

Habitat Specificity

Opercoeloides vitellosus was found in all sections of the intestine and in the rectum. It was most common in the rectum and posterior intestine, somewhat less abundant in the anterior intestine, and rare in the mid intestine (Table 4D, Fig. 8D). The amount of variation between the percentages in same gut segment of different fish can be seen by calculating their coefficients of variation. These coefficients were: intestine 1 - 185.7%, intestine 2 - 436.2%, intestine 3 - 134%, and rectum - 100%. In this species, as well as in most of the helminths studied, the coefficients of variation were inversely proportional to the abundance of parasites in a particular gut segment.

There were too few infected fish to establish any pattern of habitat selection change between the monthly samples, and since the range of intensities was so low, there was no way to study the effect of crowding.

Frequency Distribution

There were too few infected fish, and too much variation between months, to fit effectively a frequency distribution. The high variance mean ratio did indicate that such a distribution would be overdispersed.

Lecithaster confusus

Lecithaster confusus was found in the intestine and rectum of

Liopsetta for a short time in the late spring and early summer. Their appearance coincided with a spring pulse in copepod abundance, both in the estuary as a whole and in the gut contents of the fish.

Seasonal Periodicity (Table 12)

In 1975 the trematodes were found only in the month of May, and were not common. The intensity and prevalence for May were not significantly different from the other months. The members of the 1975 year class were not parasitized by Lecithaster in 1976.

The 1976 year class of flounder were parasitized by L. confusus in May and June. The prevalence and intensity of the trematodes were unchanged in these two months, then declined significantly in July. The pattern of occurrence of Lecithaster in the 0+ age group was very similar in 1975 and 1976, namely a very short pulse in the late spring. The parasites were significantly more abundant in 1976. This was a departure from the pattern shown by most of the other helminths, which tended to be more common in 1975.

None of the L. confusus found in 1975 class flounder were mature. However, in 1976, 20.3% and 25% of the worms were mature in May and June respectively.

The absence of Lecithaster in fish of the 1975 year class in May, 1976, is conspicuous, since the trematodes were present during that month in the 1976 year class. This difference in occurrence is statistically significant in terms of both intensity and prevalence of infection.

Habitat Specificity

Lecithaster were found in all sections of the intestine and the rectum, however they were most common in the posterior intestine (Table 4E, Fig. 8E). The coefficients of variation for these segments

TABLE 12

Monthly Mean Intensity (± S.D.) and Prevalence of *Lecithaster confusus* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0.2 ± 0.4	20	-	-	-
June	10	0	0	-	-	-
July	10	0	0	-	-	-
Aug.	10	0	0	-	-	-
Sept.	10	0	0	-	-	-
Oct.	10	0	0	-	-	-
Nov.	10	0	0	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0	0	-	-	-
April	9	0	0	-	-	-
May	7	0	0	7	7.9 ± 8.0	71.4
June	-	-	-	10	1.2 ± 0.9	80
July	-	-	-	10	0	0
Aug.	5	0	0	10	0	0
Sept.	5	0	0	10	0	0
Oct.	6	0	0	10	0	0
Nov.	6	0	0	10	0	0
Dec.	5	0	0	10	0	0

were: intestine 1 - 176.7%, intestine 2 - 141.9%, intestine 3 - 85.2%, and rectum - 257.3%. As has been the rule, the lowest coefficients corresponded to the segments with the highest density infections.

Since the infections all occurred within a two month period, there can be no question of a seasonal change in habitat specificity. Similarly, the limited number of infected fish and the low parasite infrapopulation density precluded any consideration of crowding effects.

Frequency Distribution

The high variance to mean ratio for Lecithaster indicated that its frequency distribution was overdispersed. Unfortunately the limited number of infected fish prevented description of a particular theoretical distribution.

Spirurid larva

The nematode larva were found in the intestine and rectum of smooth flounder during the spring, summer, and fall. These animals were discovered either free in the gut lumen or burrowing in the mucosa. They appear to be the same species occasionally found encysted in the mesenteries or on the liver.

Seasonal Periodicity (Table 13)

In 1975, the nematodes were not found in the newly metamorphosed flounder in the May sample, but were present in low numbers in June, July and August. The mean intensity of infection rose during the fall, bur this increase was not statistically significant. Collections of young fish were not made between December and February, 1976, but the nematodes were not present in older fish collected over the winter months. The worms were also not present in the March sample of 1975 year class fish. It seems likely that the nematodes were absent, or at least rare, during

TABLE 13

Monthly Mean Intensity (± S.D.) and Prevalence of *Spirurid larva* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0	0	-	-	-
June	10	0.2 ± 0.4	20	-	-	-
July	10	0.1 ± 0.3	10	-	-	-
Aug.	10	0.1 ± 0.3	10	-	-	-
Sept.	10	1.1 ± 1.9	50	-	-	-
Oct.	10	3.2 ± 3.3	70	-	-	-
Nov.	10	3.4 ± 7.4	60	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	0	0	-	-	-
April	9	0.1 ± 0.3	11.1	-	-	-
May	7	0	0	7	0	0
June	-	-	-	10	0.3 ± 0.5	30
July	-	-	-	10	0.1 ± 0.3	10
Aug.	5	0.8 ± 1.1	40	10	0.1 ± 0.3	10
Sept.	5	0	0	10	1.0 ± 1.6	40
Oct.	6	0	0	10	2.8 ± 5.2	40
Nov.	6	0.2 ± 0.4	16.7	10	0.2 ± 0.4	20
Dec.	5	0.6 ± 0.9	40	10	0.2 ± 0.4	20

the winter. The decline between November 1975 and March 1976 was a significant one. The worms were discovered at a low level in April, 1976, but were absent from the May sample. Of the months in 1976 in which yearling fish were sampled, nematodes were present in August, absent in September and October, and present again in November and December. In none of these months was there a statistically significant change in either prevalence or intensity.

Contrary to the usual situation, the 1975 pattern of nematode prevalence was more distinct than that shown by intensity. The low percentages of infection during May, June, July, and August rose significantly in September, October, and November. This fall pulse in the infrapopulation density was suggested by the intensity data, but not statistically validated.

The monthly intensities of spirurid larve in 0+ age group flounder did not vary significantly in 1976. As in 1975, there was a tendency for the mean values to increase in the fall. The prevalence of nematodes also showed this tendency, but unlike 1975, there was no significant change. There was no significant difference between the infections found in the 0+ age group in 1975 and 1976. Although the yearlings did not show as distinct a pattern as the 1976 year class, there were no significant differences between the parasites of the different age hosts.

Habitat Specificity

Spirurid larvae were found in all sections of the intestine, and in the rectum. It was however, rare in the latter organ, and most common in the anterior intestine (Table 4F, Fig. 8F). The coefficients of variation calculated for the percentages in each gut segment of the

individual hosts were: intestine 1 - 67%, intestine 2 - 117.4%, intestine 3 - 398.6%, and rectum - 616.3%.

There were not enough values to distinguish any monthly changes in habitat specificity, however the flounder were sorted according to the total number of nematodes (Table 14). Contrary to the usual situation, in this case the higher intensity infections were more concentrated in the anterior intestine.

Frequency Distribution

Although the monthly samples were not shown to be significantly different in intensity, the differences were of sufficient magnitude to preclude the lumping of samples to form a frequency histogram. The distribution was contagious, but a more precise description was not possible.

Stephanostomum tenue

Stephanostomum tenue is found in smooth flounder as a metacercaria, occurring primarily in the pericardial cavity. Since this is a resting stage the individual worms remain in their host for an indefinite period, generally far longer than those forms which mature in the gut.

Seasonal Periodicity (Table 15)

In 1975, there was no significant change in either intensity or prevalence of S. tenue in any of the monthly samples for the fish of the year. Since the metacercariae are long lived, this result implies that no significant infection occurred between May and November. There was no significant change in S. tenue abundance over the winter months. In fact, the prevalence and intensity of S. tenue in 1975 year class flounder did not change significantly at any time during 1976. Since there was no indication of either host or parasite mortality during this period, there

TABLE 14

Effect of Crowding on Habitat Specificity. Mean percentages of Spirurid larva in each gut section of 0+ age group smooth flounder (Liopsetta putnami). Data arranged by increasing total infection. (RA = range of parasites/fish, $\bar{x}$ = mean parasites/fish, n = total fish, I = 1st third intestine, II = 2nd third intestine, III = 3rd third intestine, RC = rectum).

RA	$\bar{x}$	n	I	II	III	RC
1	1	20	50	40	10	0
2-4	2.8	10	68.4	29.2	0	2.5
5-24	10.3	8	77.6	20.5	1.9	0

TABLE 15

Monthly Mean Intensity (± S.D.) and Prevalence of *Stephanostomum tenue* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	1.2 ± 1.1	80	-	-	-
June	25	1.6 ± 1.6	64	-	-	-
July	30	1.3 ± 1.6	53	-	-	-
Aug.	30	1.3 ± 1.5	63	-	-	-
Sept.	28	1.4 ± 1.7	57	-	-	-
Oct.	30	1.5 ± 1.7	66.7	-	-	-
Nov.	30	1.3 ± 1.3	63.3	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	1.1 ± 1.0	66.7	-	-	-
April	9	1.6 ± 2.3	55.6	-	-	-
May	7	0.4 ± 0.8	28.6	7	0.1 ± 0.4	14.3
June	-	-	-	10	0.2 ± 0.6	10
July	-	-	-	10	0.4 ± 0.7	30
Aug.	5	2.4 ± 2.3	80	10	0.9 ± 1.2	50
Sept.	5	2.6 ± 3.1	80	10	0.4 ± 0.5	40
Oct.	6	1.3 ± 0.8	100	10	1.1 ± 1.0	70
Nov.	6	1.7 ± 2.3	66.7	10	1.1 ± 1.2	70
Dec.	5	1.4 ± 2.2	33	10	1.4 ± 1.8	70

was no significant infection of the yearling flounder by this parasite.

The occurrence of Stephanostomum in the 1976 year class fish was not so consistent. The mean monthly intensities rose slightly during the period May through December, but the differences were not significant. The prevalence of S. tenue did increase during 1976. Infections of flounder apparently occurred as late as August. The irregularity of the 1976 data is partially due to smaller sample sizes available during that year.

Since the yearling flounder were not infected to any degree in 1976, a comparison of the 0+ and 1+ age groups in 1976 is a comparison of the total infections for the two years. There was no significant numerical difference between these infections. Comparison of the infections in fish of the year for both years showed no significant difference.

Habitat Specificity

The majority of S. tenue (94.7%) were found in the pericardial cavity of Liopsetta. The remainder were either encysted just outside the pericardium (in the coelom) or in the liver.

Frequency Distribution

Since there was no significant change in intensity during the 1975 sampling season, it was possible to combine the monthly samples in order to describe the frequency distribution of S. tenue (Fig. 12). The data were successfully fitted to the negative binomial ($X^2 = 6.06$, df = 5) when all expected frequencies less than one were combined. The estimated value of k was 1.68.

Cryptocotyle lingua

Cryptocotyle lingua is a metacercaria found in the fins and

infrequently in the skin of smooth flounder. It was rare in 0+ age group fish in the Lamprey River.

Seasonal Periodicity (Table 16)

The metacercariae were not found in 1975 year class flounder until October and November, and then at low levels. Any occurrence of this parasite in the Lamprey River is surprising, since the littorine gastropods which serve as its intermediate hosts have never been found at this collecting site. The nearest points from which these snails have been collected are Adams Point (Durham) and Fabyan Point (South Newington (Fig. 1).

In contrast to most parasite species, there was a significant increase in C. lingua abundance over the winter months. The change occurred at some time between the November 1975 and March 1976 samples. There was no further significant change for the remainder of the year. The 1976 year class showed a similar pattern. The metacercariae were not present until December, and then at a level not significantly greater than the preceeding months. Since the snail intermediate hosts are not present in the area, this increase in abundance may be due to a movement of infected fish into the Lamprey collecting site. This movement of fish apparently occurs only during the winter months. The winter increase in Cryptocotyle would be, therefore, only an artificat of smooth flounder biology. It does, however, serve as an example of the use of a parasite as a biological tag of fish movement.

Habitat Specificity

No formal system for locating these metacercariae was used, however they were found frequently on the caudal fin.

TABLE 16

Monthly Mean Intensity (± S.D.) and Prevalence of

Cryptocotyle lingua in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0	0	-	-	-
June	10	0	0	-	-	-
July	10	0	0	-	-	-
Aug.	10	0	0	-	-	-
Sept.	10	0	0	-	-	-
Oct.	10	0	0	-	-	-
Nov.	10	0.2 ± 0.4	20	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March.	9	1.1 ± 1.4	55.6	-	-	-
April	9	3 ± 7.5	44.4	-	-	-
May	7	0.9 ± 0.9	57.1	7	0	0
June	-	-	-	10	0	0
July	-	-	-	10	0	0
Aug.	5	0	0	10	0	0
Sept.	5	0.8 ± 0.8	60	10	0	0
Oct.	6	1.2 ± 1.2	66.7	10	0	0
Nov.	6	1.8 ± 2.2	50	10	0	0
Dec.	5	3.0 ± 2.5	80	10	0.4 ± 1.3	10

Frequency Distribution

The distribution of C. lingua in Liopsetta was contagious, however too few hosts were parasitized to permit a more precise description.

Protancyrocephaloides liopsettae

Protancyrocephaloides liopsettae is a monogenean parasitic solely on the gills of smooth flounder. It occurred during a brief period in the spring.

Seasonal Periodicity (Table 17)

Since this parasite was found only during the spring, it did not occur in the 1975 year class until 1976. The species, however, was noted on 1974 year class fish collected during the spring of 1975. At this time the prevalence of the trematode was 100% in fishes collected in March and April, and 0% in May and all other months. Collections during this period were made once a month.

In spring 1976, collections were made more frequently to more closely examine the occurrence of P. liopsettae. The prevalence of infection for three collections made in March was 0%, 33%, and 100% for collections on the 14th, 24th, and 31st, respectively. The overall prevalence for the month was 36.4%. Two flounder samples during April gave a combined prevalence of 90.9% infection. In May, samples on the 13th and 30th showed a prevalence of 60% and 0% respectively. The intensity of infection increased significantly between March and April and decreased significantly between April and May. There were no P. liopsettae found during 1976 other than during these months. The termatode undergoes a very rapid cycle, infecting nearly all of the fish population within a short time, and disappearing just as quickly. A seasonal abundance cycle

TABLE 17

Monthly Mean Intensity (± S.D.) and Prevalence of *Protancyrocephaloides liopsettae* in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	0	0	-	-	-
June	10	0	0	-	-	-
July	10	0	0	-	-	-
Aug.	10	0	0	-	-	-
Sept.	10	0	0	-	-	-
Oct.	10	0	0	-	-	-
Nov.	10	0	0	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	11	2.0 ± 2.7	36.4	-	-	-
April	11	3.5 ± 3.1	90.9	-	-	-
May	7	1.6 ± 2.3	42.9	7	0	0
June	-	-	-	10	0	0
July	-	-	-	10	0	0
Aug.	5	0	0	10	0	0
Sept.	5	0	0	10	0	0
Oct.	6	0	0	10	0	0
Nov.	6	0	0	10	0	0
Dec.	5	0	0	10	0	0

such as this, especially the complete disappearance of adults, is very unusual among the Monogenea.

The maturation cycle of P. liopsettae closely approximated its occurrence cycle. The animals were nearly all mature. Of the samples on the 24th and 31st of March respectively, 85.7% and 90.9% of the trematodes were mature. All subsequent collections revealed animals of similar size and gonadal development, which were all considered to be mature adults. This pattern suggested a rapid single wave of infection, and rapid growth. The parasites infected almost all the flounder within a two week period late in March. There was no evidence that any of the eggs shed in 1976 developed immediately into infective larvae. No such young stages were observed in nature, and eggs maintained in the laboratory at various temperatures failed to develop.

The usual age comparison between 0+ and 1+ age groups in 1976 was not possible since the 1976 year class had not metamorphosed during the brief appearance of P. liopsettae. Some older fish were, however, collected during 1975 and 1976. The monogenes were found on flounder of the 2+ and 3+ age groups (up to 20 cm in total length). They were not found on any older fish (5+ age group, up to 33 cm total length).

Habitat Specificity

Protancyrocephaloides liopsettae were found in the buccal cavity, most frequently on the filaments of the gill arches. In a few instances the trematodes were attached to the hypobranchial or basibranchial regions of the gill.

The spatial distribution of Protancyrocephaloides was organized on two levels. On the first level, individuals had a pronounced tendency to aggregate. The entire complement of parasites on one fish were found

frequently attached to one or two adjacent gill filaments. This clumping is a strong indication of active site selection by the parasites. The animals are of sufficient size that individuals attached to similar areas on adjacent gill arches could maintain close physical contact.

The second level of organization involved the precise placement of parasites on particular gill arches. This included the distribution of trematodes on the left and right sets of gill arches, on one of the four gill arches front to back on either side, and on the different portions of the individual arches.

The parasites were not evenly distributed between the left and right sets of gill arches. The left side of the fish is down when the flounder is oriented on the bottom, and in 1976, fully 70% of the trematodes were found on the left side gill arches. Of the 32 fish infected, P. liopsettae were found on the left side gill arches only in 22 cases, on the right side only in four cases, and in six instances on both sides at once. The tendency for the animals to clump distorted the probability of trematodes being found on both sides at once, so I considered only those fish where the parasites were found on one side or the other. For these 26 cases, the expected frequencies for a 1:1 split would be 13 left and 13 right. The observed frequencies were significantly different ($X^2 = 12.5$, df = 1).

The distribution of P. liopsettae on the four gill arches was also unequal. In 1976, there were no parasites found on the two most posterior arches on either side. I found 88.1% of the animals on one of the first arches, and 11.9% on the second arches. On the first two arches on the left side, the trematodes were attached on the first arch only in nine cases, never on the second arch only, and in three cases on both first

and second. In those cases where the trematodes were found on one arch or the other, there was a significantly greater number of parasites on the first arch than on the second. Of the five fish carrying trematodes on their right side gill arches, four bore them on the first and one on the second arch. The trend is clear, but not statistically significant due to the small sample size.

In addition to the side to side and front to back orientations, P. liopsettae also occurred more frequently on certain areas of the individual gill arches. To quantify this orientation, each arch was arbitrarily divided into dorsal, medial, and ventral areas (Fig. 13), and the number of trematodes counted (Table 18). For the monogenes occurring on the first gill arches, 78.8% were found on the ventral areas, 21.2% on the medial areas, and none on the dorsal portions. Of the 14 fish found with trematodes on their first left gill arch, the worms were found on the ventral area 10 times, and four times on the medial area. This is a statistically significant ($X^2 = 10.9$, df = 2) departure from equal frequencies on the three sections of this arch. Although the first right gill arch was only infected in four fishes, in all cases the parasites were found in the ventral area. This also is statistically significant ($X^2 = 8.03$, df = 2). All parasites on the second gill arches occurred on medial or ventral areas, but their small number precluded any statistically significant difference.

Reflecting their tendency to clump, in no instance were trematodes found in more than one portion of an individual gill arch. A second consequence of clumping is the tendency, when parasites were found on both first and second gill arches, for the animals to occur on the same section of both. This pattern was seen in Table 18 for fish 76-5, 76-13, and 76-24.

TABLE 18

Position of Protancyrocephaloides liopsettae on the gills of 1+ age group smooth flounder. Spring 1976. (D, M, and V are the dorsal, medial, and ventral portions of a gill arch).

		Right Side						Left Side					
		Arch 1			Arch 2			Arch 1			Arch 2		
FISH I.D. #	TOTAL INFECTION	D	M	V	D	M	V	D	M	V	D	M	V
76-5	3	0	0	0	0	0	0	0	0	2	0	0	1
76-7	4	0	0	3	0	0	0	0	0	0	0	0	1
76-11	7	0	0	3	0	0	0	0	0	4	0	0	0
76-12	4	0	0	0	0	0	0	0	0	4	0	0	0
76-13	3	0	0	0	0	0	0	0	0	2	0	0	1
76-15	1	0	0	0	0	0	0	0	0	1	0	0	0
76-16	1	0	0	0	0	0	1	0	0	0	0	0	0
76-17	12	0	0	9	0	0	0	0	0	3	0	0	0
76-18	3	0	0	0	0	0	0	0	3	0	0	0	0
76-19	3	0	0	0	0	0	0	0	0	3	0	0	0
76-21	1	0	0	0	0	0	0	0	0	1	0	0	0
76-22	5	0	0	3	0	0	0	0	0	2	0	0	0
76-23	1	0	0	0	0	0	0	0	0	1	0	0	0
76-24	6	0	0	0	0	0	0	0	3	0	0	3	0
76-29	3	0	0	0	0	0	0	0	3	0	0	0	0
76-33	2	0	0	0	0	0	0	0	2	0	0	0	0
Total	59	0	0	18	0	0	1	0	11	23	0	3	3
Mean	3.7	0	0	1.1	0	0	0.1	0	0.7	1.4	0	0.2	0.2

In all three cases the monogenes on the adjacent arches were effectively members of a single "clump".

Frequency Distribution

The distribution was overdispersed, but there were too few data points to fit a specific pattern.

Glugea stephani

Glugea is a microsporidan protozoan parasite, the cysts of which were found in the gut wall and viscera of smooth flounder.

Seasonal Periodicity (Table 19)

Glugea was not present in the May 1975 sample of 0+ age group smooth flounder. There was, however, a low level infection in June, and a significant increase in July. The prevalence decreased significantly in August. This was unusual since the life span of Glugea in flounder is long, and its prevalence would not decrease over a period as short as one month. The infections were light enough to exclude the possibility of mortality. One explanation for the August decline could be dilution of the Lamprey River stock by fish from some less infected area. After August, there was no significant change in prevalence for the remainder of the season, but the extent of infiltration and the number and size of Glugea cysts did increase in the fall. Some of the young flounder were infected heavily by this parasite, although the infections were not generally as severe as those of the winter flounder, Pseudopleuronectes americanus.

Glugea infections in the 1975 year class did not change significantly over the winter of 1975-1976, and remained the same over the entire 1976 collecting season. In the fall of 1976, the prevalence of the parasite was not significantly different between the 1975 and 1976 year classes.

The 1976 year class flounder were not infected by Glugea in

TABLE 19

Monthly Mean Intensity (± S.D.) and Prevalence of

Glugea stephani in 1975 and 1976 year class smooth flounder

	1975 Year Class			1976 Year Class		
Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	-	-	0	-	-	-
June	-	-	20	-	-	-
July	-	-	66.7	-	-	-
Aug.	-	-	33	-	-	-
Sept.	-	-	35.7	-	-	-
Oct.	-	-	47	-	-	-
Nov.	-	-	53.4	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	-	-	55.6	-	-	-
April	-	-	-	-	-	-
May	-	-	-	7	-	0
June	-	-	-	10	-	10
July	-	-	-	10	-	20
Aug.	-	-	40	10	-	30
Sept.	-	-	40	10	-	70
Oct.	-	-	50	10	-	30
Nov.	-	-	33.3	10	-	30
Dec.	-	-	40	10	-	20

May, 1976. They were infected in June, July and August, but the most significant increase occurred in September. The infection rate then declined over the remainder of the year. As in 1975, this decline is difficult to explain in a static host population.

Habitat Specificity

Glugea was never found in the stomach wall. The cysts in some cases were distributed evenly in the intestinal and rectum walls and in others they were concentrated in particular areas.

Cryptobia bullocki

Cryptobia bullocki is a blood flagellate found in several species of estuarine fishes, including both smooth and winter flounder.

Seasonal Periodicity (Table 20)

The infestation of the 0+ age group flounder was very similar in 1975 and 1976. The parasites were not found in the young fish until the fall (September and October for 1975 and 1976 respectively). The prevalence increased significantly in November, 1975, but in 1976 it remained at a low level through December. While samples could not be made over the winter months, the presence of the parasite in older age groups during this time proved that it is not temperature limited.

The prevalence of C. bullocki did not change over the winter of 1975-76, but increased rapidly in March and April until virtually all yearling fish were infected. This rate of infection remained for the rest of the year. In the fall of 1976, the 1975 year class flounder were much more heavily infected than the 1976 fish.

Unidentified Sporozoan #1 (Table 21)

In heavy infections this parasite was observed as a sporozoite (merozoite) stage in the flounder intestine. It is likely that low

TABLE 20

Monthly Mean Intensity (± S.D.) and Prevalence of

Cryptobia bullocki in 1975 and 1976 year class smooth flounder

Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	-	0	-	-	-
June	25	-	0	-	-	-
July	30	-	0	-	-	-
Aug.	30	-	0	-	-	-
Sept.	28	-	10.7	-	-	-
Oct.	30	-	20	-	-	-
Nov.	30	-	53.4	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	-	55.6	-	-	-
April	9	-	77.8	-	-	-
May	7	-	100	7	-	0
June	-	-	-	10	-	0
July	-	-	-	10	-	0
Aug.	5	-	80	10	-	0
Sept.	5	-	100	10	-	0
Oct.	6	-	67	10	-	20
Nov.	6	-	83.4	10	-	30
Dec.	5	-	60	10	-	0

TABLE 21

Monthly Mean Intensity (± S.D.) and Prevalence of

Unidentified sporozoan #1 in 1975 and 1976 year class smooth flounder

Month	n	Mean ± S.D.	Prevalence (%)	n	Mean ± S.D.	Prevalence
May	5	-	0	-	-	-
June	10	-	0	-	-	-
July	10	-	10	-	-	-
Aug.	10	-	60	-	-	-
Sept.	10	-	30	-	-	-
Oct.	10	-	10	-	-	-
Nov.	10	-	90	-	-	-
Dec.	-	-	-	-	-	-
Jan.	-	-	-	-	-	-
Feb.	-	-	-	-	-	-
March	9	-	0	-	-	-
April	9	-	11.1	-	-	-
May	7	-	28.6	7	-	28.6
June	-	-	-	10	-	30
July	-	-	-	10	-	30
Aug.	5	-	0	10	-	80
Sept.	5	-	0	10	-	70
Oct.	6	-	16.7	10	-	40
Nov.	6	-	16.7	10	-	60
Dec.	5	-	80	10	-	70

intensity infections were overlooked, and for this reason the prevalence of the parasite was only a relative measure, and should be considered to be a minimum value. The variability of the data renders interpretation difficult. The intensity of the infections was also variable. It did not, however reach extraordinarily high levels, and no pathology was ever apparent. There were no samples during the winter of 1975-76, however the prevalence declined significantly over this period. The abundance of the sporozoan remained low in the yearlings until a sudden significant increase in December of 1976. Despite this increase, there were significantly fewer yearlings infected than fish of the 1976 class.

Unidentified Sporozoan #2

The second unidentified sporozoan (Eimeria anguillae?) occurred during a restricted time period. It was found in the intestine and rectum of yearling flounder during the winter and spring. In March and April, 1976, the prevalence of the parasite in yearlings was 55.5% and 44.4% respectively. It was not found during any other months, and never infected the fish of the year. The intensity of infection was high in some cases (Fig. 3), however there was never any indication of sexual reproduction or pathology.

Miscellaneous Metazoa

There were two metazoans which, although they occurred very rarely, appeared to follow some seasonal pattern of abundance. These species are mentioned briefly below.

Proteocepholid plerocercoid

These animals were found in the intestine and rectum of 0+ age group flounder in May, 1975, and May and June, 1976. Their prevalence was 40%, 42.9%, and 10% respectively during these months. The larvae never

showed any sign of development, and the mean intensity of the infections was fewer than one per fish.

Argulus laticauda

This branchiuran ectoparasite was found on the skin of the flounder during spring and summer. Twenty percent of the 0+ age group were infected in May of 1975. All other argulid infections occurred during the months of July and August. In 1975, the prevalence in the 0+ age group was 10 and 30%, respectively, for these months. In July 1976, 10% of the 1976 year class were parasitized, and 60% of the yearlings were infected in August. The occurrence of A. laticauda was uneven, varying sharply between months and year classes. The mean intensity of infection was in all cases less than one.

Correlations

The extent to which two parasites vary together in number can be expressed as a correlation coefficient.

The correlations of one species to another which were significant at the 5% level are given in Table 22, along with their calculated Spearman's rank correlation coefficients (r).

The most common and consistently significant correlation was the positive one between Lepocreadium and Zoogonus, which occurred five times. Lepocreadium and Opecoeloides had a significant negative correlation on two occasions. Zoogonus and Glugea were correlated three times, but the significance of these interactions was lessened since two were negative and one positive. The two significant correlations of S. tenue and Glugea also differed in sign. All other significant correlations occurred one time only.

TABLE 22

Significant Spearman's Rank Correlation Coefficients (r)

Calculated for 1975-76 monthly samples

1975	1975 class	1976 class
May	none	-
June	none	-
July	L. setiferoides-Z. lasius = .848	-
	Glugea-Z. lasius = .697	-
August	L. setiferoides-Z. lasius = .794	-
	L. setiferoides-O. vitellosus = -.674	-
Sept.	none	-
Oct.	L. setiferoides-Z. lasius = .745	-
	S. tenue-Glugea = .854	-
Nov.	L. setiferoides-S. tenue = -.704	-
	Z. lasius-C. bullocki = -.740	-

1976		1976	
March	S. tenue-Glugea = -.810	May	none
April	Z. lasius-S. tenue = -.725	June	L. setiferoides-O. vitellosus = -.767
	Z. lasius-Glugea = .750		
	C. lingua-P. liopsettae = .806	July	O. vitellosus-S. tenue = 0.786
May	none		
August	H. pallidum-O. vitellosus = 1.0	Aug.	L. setiferoides-Z. lasius = 0.719
Sept.	none		
		Sept.	L. setiferoides-Z. lasius = 0.685
Oct.	Z. lasius-Glugea = -.933		
Nov.	C. bullocki-spirurid larva = -1.0	Oct.	S. tenue-Spirurid larva = 0.741
Dec.	none		
		Nov.	none
		Dec.	none

Discussion and Conclusions

Seasonal Periodicity

Parasite seasonal abundance can be measured by changes in intensity (number of parasites/host) or prevalence (percentage of hosts infected). These quantities, however, do not always vary consistently. Kennedy (1969) cited instances where changes in intensity were superimposed on continuously high levels of parasitism. This is not surprising, since in high level infections intensity may still vary after prevalence has reached its upper limit (100%).

In the present study, almost all metazoa exhibiting seasonal periodicity varied in essentially the same pattern for both measures. Lepocreadium setiferoides, however, demonstrated the pattern described by Kennedy. Between June and November, 1976, all samples of 0+ age group smooth flounder were 100% infected with the parasite. During the same period, intensity varied significantly. It is clear from such results that while both intensity and prevalence are appropriate for seasonal abundance studies, the former measure is more sensitive in high intensity infections.

The parasites of Liopsetta can be divided into those occurring year round in the fish and those which did not. The latter group was larger, and by definition underwent seasonal abundance changes. The abundance of some of the first group also varied seasonally. Some common species occurring in Liopsetta for only a part of the year were H. pallidum, O. vitellosus, L. confusus, the spirurid larvae, P. liopsettae, and the unidentified sporozoans #1 and #2. The year round parasites of Liopsetta were L. setiferoides, Z. lasius, S. tenue, C. lingua, G. stephani and

C. bullocki. These species varied greatly in their seasonal abundance cycles. Lepocreadium and Glugea exhibited definite seasonal cycles of abundance. The cycle discovered for Lepocreadium corresponded roughly to that found by Magendantz (1969), who reported the highest prevalence and intensity in July and August (or 1 to 2 months earlier than the present study). Her highest prevalence and intensity values (50-90% infected, 50-100 worms/fish) were also comparatively low. This could be a result of differences between collecting sites and/or between years sampled, both of which affect parasite abundance.

S. tenue and C. lingua are metacercariae in flounder, and therefore their long life obscures most seasonal variation in density. Stephanostomum, however, was recruited during a limited time in spring and summer, and therefore qualifies as a species with a seaonal cycle. Cryptocotyle is precluded effectively from debate concerning its cycle, since all changes in density at the Lamprey River appear to result from host migration. Of all the common parasites of smooth flounder, only Z. lasius and C. bullocki did not exhibit some seasonal periodicity (Tables 9 and 20). This finding for Cryptobia corresponds to the findings of Strout (1962). The preponderance of fish parasite species showing some seasonal change in abundance was mentioned by Kennedy (1977).

Interpreting seasonal periodicity from field data is difficult. Firstly, the life spans of the parasites in flounder are not known. The species occurring for only a portion of the year place an upper limit on their longevity, and Esch et al (1977) stated that helminths generally live less than one year. These rough estimates, however, are of little value in interpreting abundance data. Explaining such data is also hindered by lack of knowledge of the parasite infrapopulations in other

hosts (e.g. cercariae shed from snails, encysted in polychaetes, etc.) Without abundance data from these sources, the population dynamics of most flounder parasites form only a portion of the picture.

Within these limitations, certain factors are considered to be of primary importance in influencing seasonal parasite fluctuations. Kennedy (1970; 1975) reviewed these factors and concluded that most changes can be correlated with variations in fish behavior and diet, directly or indirectly with physical changes in the water, and especially with temperature (Kennedy, 1977).

For organisms in an estuary, the most conspicuous physical change in the water (aside from temperature) is in salinity. In the Lamprey River it would be difficult to separate the effects of temperature and salinity, since the two factors varied seasonally in a similar way (Figs. 6 & 7). Samples at different stations, where salinity fluctuations were not as marked, have emphasized the pre-eminent role of temperature.

Evaluating changes in fish behavior is beyond the scope of this dissertation. However, a circumstance which might be attributed to either behavior or food availability is the lack of food in fish guts during the winter. It isn't known if this situation resulted from reduced feeding activity (i.e. behavior) or whether food was not available. There is, however, a definite correspondence to the winter decrease in most helminth parasites.

To monitor the diet of smooth flounder, the stomach contents of the fish necropsied for parasite analysis were observed. The food habits of smooth flounder were considered in detail in Part I. The most common food items were small polychaetes of the genus Polydora, bivalves (Mya arenaria, Tellina agilis), and gastropods (Hydrobia spp., Odostomia sp.,

Mitrella lunatia). The polychaetes especially were common and can serve as intermediate hosts. Unfortunately, this information is of little use in interpreting seasonal cycle data, since parasites such as Lepocreadium, Homalometron, and Zoogonus all use such worms as second intermediate hosts, and have different seasonal cycles. It is difficult to correlate a single common food item with three different life cycles, and this is the situation for most of the common parasites.

Lecithaster confusus is one species where the diet of smooth flounder can probably be related to the seasonal abundance of the parasite. The reported second intermediate host, the copepod Acartia tonsa, was never found in the gut of smooth flounder, but is present in the Great Bay estuary (Croker, 1972). The occurrence of Lecithaster in late spring corresponded with a bloom of copepods in the estuary, and with their common occurrence in the gut of the flounder. The spring is the only time when copepods were the dominant food item of young flounder, and this diet probably resulted in the acquisition of Lecithaster. The trematodes disappeared when the fish returned to eating annelids and molluscs.

I have mentioned host behavior and diet as factors which contribute to the seasonal abundance cycles of fish parasite populations. Neither of these factors, however, are independent of temperature. Temperature is the master factor, and it operates by affecting rates of infection, rather than by influencing parasite mortality (Kennedy, 1975). Infection rates can be influenced by controlling parasite reproduction, the availability of infective larvea, or the establishment of the parasite. Unfortunately, while temperature undoubtedly affects the parasites of smooth flounder, the life cycles of most species are too complex to demonstrate the method. This is not the case for Protancyrocephaloides

liopsettae. This monogene does not have an intermediate host, and the larvae apparently hatch from eggs which have lain dormant since the previous spring. In both 1975 and 1976, the appearance of P. liopsettae in late March corresponded closely with the first increase in water temperature following ice off. The monogene appeared around the estuary, in areas of widely disparate salinity, just as the temperature started to rise. In both years the trematode disappeared in early May, before water temperatures reached 15°C. While laboratory evidence would be necessary to prove the relationship, the field data strongly indicate a temperature-occurrence relationship for Protancyrocephaloides. Temperature in this case influenced the infection rate by controlling the availability of infective larvae.

It is unusual for a monogene like P. liopsettae to be abundant for such a small proportion of the year (6 weeks), and then absent for the remainder. This is especially true when the period of absence includes the warm summer months. The only comparable case was reported by Davies (1967, cited in Kennedy, 1970), who found four species of Dactylogyrus with similar cycles. The reason this pattern of occurrence is so unusual is that it requires the presence of a resting (or diapause) egg. A monogene egg which fails to develop at low temperatures (< 5°C) has been demonstrated by Paling (1965). In the present case, however, the eggs apparently lie dormant through the summer, autumn, and winter, to hatch finally when the temperature rises the following spring. Such eggs would represent a more refined system than simple low temperature mediated dormancy, but their existence in the Monogenea is controversial. Paperna (1963) hypothesized diapause eggs, but Crane and Mizelle (1968) stated that none had every been demonstrated. Since attempts to maintain P. liopsettae eggs in the laboratory were not successful, the question was

not settled. For Protancyrocephaloides, however, an alternative to diapause eggs is not apparent.

Initial Acquisition of Parasites

The initial acquisition of a parasite fauna followed a similar pattern in both 1975 and 1976 for 0+ age group smooth flounder. The young fish were infested with similar parasite species, almost all of them conforming to characteristic patterns of seasonal occurrence. The only species varying significantly was Stephanostomum tenue, which was infective for a longer period in 1976. The reason for this difference is not known.

While patterns of acquisition were similar, there were differences in the magnitude of infections between 1975 and 1976. Of the eleven species compared, six were not significantly different, three were more common in 1975, and two were more abundant in 1976. There were few common denominators within these groups. The species which were more (or less) abundant do not share any intermediate hosts, etc., and no ecological reasons for the differences are apparent. The existence of differences between the two years was not unexpected, however; Kennedy (1977), in considering the regulation of fish parasite populations, concluded that "most fish parasites are unstable and unregulated". He stressed that regulation, even when identified, was commonly density independent and thus unlikely to achieve stability over a period of time. Indeed, the models of Anderson (1974a and b; 1976) predict long term oscillations due to chance alone. Considering these factors, the observation of yearly changes in parasite abundance is not surprising, if as yet unexplained.

The Effect of Host Age

The differences in parasite fauna between different age hosts have been known for some time. Gorvunova (1936; cited in Dogiel, 1956) divided the parasites of Esox lucius and Rutilus rutilus into those species independent of host age (33.3% of the total), those which increased with host age (55.5%), and those which decreased (11.1%).

Only two age classes (0+ and 1+) of Liopsetta were examined, but the trend was similar to that observed by Gorbunova. In 1976, there was no significant differences in parasitism between the age groups for six species (50%), four species (33.3%) increased in older fish, and two species (16.7%) decreased in older fish. Considering the size and habitat similarities of the age groups, it is not surprising that the largest group of parasites was that showing no differences. The trend, however, was definitely toward a greater number and variety of parasites in the older fish. In addition to there being more species which increased rather than decreased, the increasing species included the dominant helminth (L. setiferoides), and Z. lasius. The parasites which decreased (Lecithaster confusus and the unidentified sporozoan #1) were relatively unimportant.

The causes of age related changes in parasite fauna are only generally known. Dogiel (1956) correlated such changes with those in the host's diet, habitat, and overall ecology. He noted also that larger and older fish ate more, and thus acquired a larger number of parasites via intermediate hosts. The parasites of Liopsetta provide examples of both of these mechanisms. Lecithaster confusus, for example, was one of the species more common in the 0+ age group. The absence of this trematode from the larger 1+ age group flounder indicated that these animals were

not eating the copepod which carries L. confusus.

An increased volume of food was the probable reason for the greater numbers of Zoogonus lasius in 1+ age group flounder. The larger fish apparently consumed greater numbers of infected polychaete intermediate hosts. The situation, however, is more subtle in the case of Lepocreadium setiferoides. These trematodes were more common in the older fish, but only for the months (August and September) of greatest abundance. It is unlikely that the 1+ age group were eating more intermediate hosts during these months only. One explanation is that the larger intestine of the larger fish is capable of maintaining greater numbers of trematodes. A controlled experiment would be necessary to verify this hypothesis, but Lepocreadium is the only parasite of Liopsetta which reached densities which might be self-limiting.

Host Biology

In addition to the basic information about fluctuations in parasite abundance, the year round study of a parasite fauna can provide information on the biology of the host. The occurrence of Cryptocotyle lingua and Glugea stephani is an example of such information. The problem with finding C. lingua in the Lamprey River is that since the snail intermediate host does not occur in the river, infections of fish cannot occur there. The presence of the parasite indicated that flounder infected elsewhere moved into the area. The parasite increased in abundance in the late fall, and winter of the first year of the flounder's life. This increase indicated a movement of fish from the lower estuary into the river. The movement could have been part of a general mixing of stocks from all areas of the bay, but parasite data are insufficient to answer this question.

The situation was similar for G. stephani. The problem is the significant decrease in prevalence between July and August, 1975, in the 0+ age group fish. The infection is a long term one, and the cases in question were of too low intensity to cause mortality. The most practical explanation for the decrease is an influx of uninfected or lightly infected fish. Corroborative evidence for such a migration would have to come from more traditional fish tagging methods. The decrease in Glugea prevalence did occur again in 1976, although not over so short a period of time. This recurrence improves the chance that it reflects a consistent event in the life history of the flounder.

Habitat Specificity

Different parasites tend to be distributed differentially within the flounder gut (Fig. 8). The absence of all helminths species from the stomach is not surprising, since the low and variable pH, variable osmotic pressure, and digestive enzymes of this organ limit the parasite fauna to nematodes and a few trematodes (especially the family Hemiuridae) (MacKenzie and Gibson, 1970). All of the enteric species were found in all other areas of the flounder gut, but their distributions were not the same. Some parasites, such as the spirurid larvae, were concentrated in the anterior regions of the intestine. Others, such as Z. lasius, were most common in the rectum. The spirurid larvae and Zoogonus represent extremes of habitat specificity, but all of the enteric helminths were found more commonly in one area than in another.

The greatest difficulty in dealing with the enteric distributions of helminths was the great variability between host individuals. Species like Zoogonus and the spirurid larvae, with pronounced habitat specificities, showed less of this variation than the more evenly distributed

species. Lepocreadium was particularly variable, and this is reflected in the high coefficients of variation of the four gut sections.

The factors which influence the distribution of parasites in the host gut are complex. Some which have been implicated are the ontogenic migration of parasites (Chandler, 1939), and circadian migration of parasites (Read and Kilejian, 1969), the orientation of parasites to food in the gut (Croll, 1976), and interior intraspecific interactions (Holmes, 1961; 1962; MacKenzie and Gibson, 1970; Chappell et al, 1970; Hopkins, 1970). Of these, interspecific effects are uncommon (Holmes, 1973). The effect of food is not fully known, but since parasite distributions did not change markedly between day 0 (food present) and day 1 (food absent), its effect in this case was not great. No ontogenic movements were noted, and the differences in distribution of parasites in fish autopsied within a short time interval argue against any consistent diel changes. These results do not provide a clear explanation for the individual differences seen in a natural population. The variety seen in a particular parasite species probably is due to the combined effects of several factors such as the above. It is not likely that the processes involved can be untangled from field data alone.

The subject of seasonal variation in habitat specificity has been less well studied. MacKenzie and Gibson (1970) found seasonal habitat differences in Cucculanus minutus. MacKenzie and Gibson also found an ontogenic migration of Podocotyle sp. in Platichthys flesus which gave the appearance of a seasonal change. There is no report in the literature of a habitat change due solely to the change of seasons. In Liopsetta, the only parasite found commonly enough for a year round habitat analysis was L. setiferoides. Lepocreadium gave no evidence for a seasonal change

in its distribution (Table 5).

The effect of crowding on the distribution of parasite populations has been observed in several instances. Chappell et al (1970), and MacKenzie and Gibson (1970) reported that crowding caused helminths to spread out from their preferred habitat. In Liopsetta, this effect was apparent for L. setiferoides, Z. lasius, and H. pallidum. For the spirurid larvae, however, the tendency was to concentrate more closely in the anterior intestine. The nematodes were not extraordinarily common even at their highest densities. The low level infections may not have been sufficient to elicit the usual effect.

Outside the gut lumen, there is a different situation with regard to habitat specificity. The habitats are diverse, many of the parasite species are not motile, and the factors affecting their distribution are not as well known. The actual concept of site selection in such areas has been challenged by Croll et al (1975) and Croll (1976). These workers have emphasized the role of random forces in "selection". According to Croll (1976), their view "places greater emphasis on the plumbing and engineering of the host's organs than was previously the case". The parasites are considered to be widely distributed within the host, but to survive only in the "preferred" site.

A parasite which bridges the gap between enteric species and those found in other organs is Glugea stephani. This microsporidan is found in the gut wall and visceral organs. McVicar (1975) and Olson (1976) demonstrated that the life cycle can run directly or utilize a crustacean intermediate host. Some G. stephani infections had cysts evenly distributed in the gut wall, while in others they were concentrated in one area (e.g. the anterior intestine, rectum, etc.) The reason for these differences is not

known. One possibility is that different modes of infection might lead to such different patterns. Specifically, infection directly by spores could lead to the even distributions, and an intermediate host might contain the spores sufficiently to infect a specific portion of the gut. The arguments of Croll and his coworkers do not apply in this case, since there was no evidence of differential survival.

The remaining parasites have no connection with the gut of the fish. Cryptobia bullocki occurred in the blood of smooth flounder. There was no clear distributional pattern, and the flagellates were found in different instances more commonly in the peripheral circulation, in the heart, in the kidney, or in all these areas. I have no explanation for this variability. An additional complication arises from the possibility of an enteric cryptobiid in smooth flounder. Examination of the gut involves cutting blood vessels, and possible contamination of the gut contents. There have been instances, however, where true infections of the gut have been indicated. Stained sections of the intestine have shown no flagellates, but this is not conclusive. The intestinal form appeared morphologically identical to the blood parasites.

In addition to the uncertainty regarding flagellates in the gut, there were indications of Cryptobia in the urinary bladder of Liopsetta. My reservations about this situation are identical to those applied to the gut. It was difficult to separate a parasite which might infect the bladder (or gut) from one found only in the blood supply of that organ.

The two metacercariae infecting Liopsetta were Stephanostomum tenue and Cryptocotyle lingua. These species have very different habitats, and present different problems of specificity. Both parasites infect

their host by active penetration. The cercariae of C. lingua, however, encyst immediately upon penetration. S. tenue cercariae do not encyst until they have reached the pericardial cavity, and the precise route taken is not known. The parasites were extremely specific, being found only rarely outside of the pericardium. They can survive, however, in the liver. The S. tenue larvae are large and robust, and it is unlikely that cercariae deposited randomly in less than optimal positions would fail to develop so completely as to avoid detection. It is probable, therefore, that the habitat specificity of S. tenue results from active site selection.

Cryptocotyle lingua is found in the fins and body integument of many fish species. In Liopsetta, the metacercariae occurred most frequently in the caudal fin. In nature, this fish frequently buries its body in the sediment, but the caudal fin may be exposed. Parasites in this fin, which is thus differentially exposed to cercariae, fit Croll's description of a distribution dependent on host engineering. C. lingua occurs in many hosts, and in free swimming fish it is not specific for the tail. Its lack of both host and site specificity in these fish makes it unlikely that C. lingua actively selects a habitat. Of the two metacercariae, therefore, the evidence suggests that one selects its habitat and one does not.

The final species with which I am concerned is the monogenean Protancyrocephaloides liopsettae. The Monogenea are typically habitat specific. The work of Cerfontaine (1896, 1898) and Gröben (1940) established that members of a single genus are found consistently on certain areas of the gills. Cerfontaine believed that this specificity was due to active selection on the part of the parasite, and Franklin (1955) shared

this opinion. An opposite view was taken by Llewellyn (1956), who examined the diclodophoroidean monogeneans of 11 marine fish species. Llewellyn found habitat specificity in all parasites of which sufficient numbers were observed, but he attributed this specificity to differential infection based on the varying strength of gill ventilating currents passing over the different gill arches. Llewellyn believed that a stronger current would lead to a greater chance of infection by onchomiracidiae, but that this stronger current would also wash the parasite species off differentially, and thus lead to interspecific differences in distribution.

Llewellyn recorded the number of parasites per gill arch. More recently, Akazaki (1965), Wiles (1968), Ktari (1969), and Suydam (1971) defined the habitat specificites of different species more precisely by dividing the individual arches into different areas, and recording the precies location of the parasites. These workers found differences in distribution between the hemibranchs on each gill arch, between the dorsal, medial, and ventral regions of each arch (see Fig. 14), and between the proximal and distal regions of the individual gill filaments. The consensus of opinion what that such differences were mediated primarily by the gill ventilating current. Although lacking experimental evidence, Kennedy (1975) disagreed, stating that monogene spatial distributions were "due to parasite selection, and cannot be explained in terms of water currents".

The emphasis on the importance of water flow has led to efforts to measure these currents. One of the most ingenious methods was employed by Paling (1968), who used the glochidia of the fresh water clam Anodont acygenea to infect Salmo trutta. Since these glochidia are completely passive, their abundance on the various trout gill areas should

reflect the relative strength of the ventilating current. Paling concluded that, for the trout, the current was strongest over the second and third arches, less strong over the first arch, and least over the fourth. Unfortunately, it is not valid to extrapolate these results to other fish species, especially to asymetrical forms such as the Pleuronectiformes.

The distribution of P. liopsettae on Liopsetta was obviously heterogeneous. The parasites occurred differentially on the left and right sides of the buccal cavity, on the four gill arches front to back on either side, and on the dorsal, medial, and ventral sections of the individual arches. The left to right difference in distribution has never been reported for any other species. It is likely that this difference is a symptom of the asymetry of the fish host. MacKenzie (1970), however, studied the spatial distribution of a Gyrodactylus species on young plaice (Pleuronectes platessa), and did not find any inequality.

Despite the inequalities in parasite distribution, lack of knowledge of the smooth flounder ventilating current precludes settling the question of active vs. passive site selection in P. liopsettae. It is unlikely but possible that such a distribution could be derived from water currents alone. However, the clumping of the trematodes, so that the parasites of a single fish (up to 10-12 individuals) were frequently attached to 2 or 3 adjacent gill filaments, could not be derived from water currents alone. This clumping provides proof of active site selection by P. liopsettae, and although such clumps have not been described in the literature, they have been observed in the related monogene Urocleidus chautauquensis on rock bass, Ambloplites rupestris (Burn, unpublished data). The clumps presumably facilitate cross fertilization between these very small animals.

It is likely that the spatial distribution of P. liopsettae is determined by both active and passive behavior on the part of the mongenes. The clumping is undoubtedly active, and represents site selection on the part of the parasites. This selection clouds the interpretation of other parasite spatial distributions. The left-right orientation, however, in these flattened fish, suggests a purely passive response to the asymetry of the host. The validity of this hypothesis could be tested by examining the ventilating current of the fish.

With regard to the question of active versus passive monogene infection, the arguments advanced by different workers are frequently the result of work with one or a small group of related parasite species. Monogenes, however, are a varied group. This is especially true of the two major divisions of the subclass, the Monopisthocotylea and the Polyopisthocotylea. The former group includes many of the smaller monogenes, including Protancyrocephaloides and Urocleidus and is generally characterized by haptoral hooks and suckers which are capable of some movement. The Polyopisthocotylea, on the other hand, are larger animals frequently attaching by elaborate, clamping organelles which limit their mobility. Workers such as Llewellyn (1956) who ascribe the spatial distributions of monogenes to water currents, have worked with this order. They are probably correct in this opinion. For the Monopisthocotylia, however, species such as P. liopsettae and Urocleidus chautauquensis provide strong evidence for both active and passive components of habitat specificity.

The conclusions reached for the Monogenea can probably be extended to all the parasites of Liopsetta. Habitat specificity is determined by both active and passive parasite behavior, and that the relative component of these behaviors vary between species. While there were parasites, such

as C. lingua and Glugea stephani, whose distribution was determined by the host, there was no evidence for differential survival. In Liopsetta, then, the mechanism proposed by Croll was not accurate. The majority of the species, both in and out of the gut, showed evidence of active habitat selection. The mechanisms for such selection, however, are poorly known.

Frequency Distributions

The dispersion pattern of any animal (or plant) species can be described as either underdispersed (uniform), random, or overdispersed (clumped). In every case calculated in the present study, the variance to mean ratio exceeded one, indicating an overdispersed distribution. The work of Crofton (1971 a and b), Pennycuick (1971 b), Anderson (1974 a), and others has indicated that overdispersion is an inherent characteristic of parasite systems. Crofton (1971 b) demonstrated that overdispersion allowed for regulation of both host and parasite populations by restricting the highest intensity infections to a small number of hosts. In this situation the parasite can regulate both its and the host's population by causing the death of the host. Overdispersion is necessary for regulation, since the death of heavily infected hosts must remove a greater proportion of the parasite's population than of the host's. Esch et al (1977) suggested that overdispersion also minimizes parasite competition by maximizing the space and nutrient resources (i.e. lightly infected hosts) available for infection.

The theoretical model of overdispersion most generally applicable to helminth infrapopulations is the negative binomial (Esch et al, 1977). For the three instances in the present study in which it was possible to fit a specific frequency distribution, the negative binomial best described the data. This distribution was especially useful since Crofton demonstrated

that it can be regarded as a fundamental model (i.e. the theoretical background of the distribution can be related to biological phenomena). A fundamental model is based on a hypothesis of biological significance, and if it is fitted successfully, it provides justification for this hypothesis.

Crofton (1971 a) provided a list of biological hypotheses from which a negative binomial distribution of parasites might arise. Pennycuick (1971 b) presented a slightly amended version of the list. Her possible hypotheses were:

1. The host is exposed to several waves of infection, each of which attacks randomly, giving rise to a series of Poissons.
2. The infective stages of the parasites are not randomly distributed.
3. The presence of a parasite in a host increases or decreases its chances of acquiring further infections.
4. The sampling units are bit equal; for example, the hosts are of different ages.
5. The sampling units change during sampling; e.g. if the sampling takes a long time, the ages of the hosts will change
6. The distribution sampled is not homogeneous but clumped.

The factors which lead to a particular negative binomial are hard to define from field data. Not knowing the dispersion pattern of the fish host, any intermediate hosts, or the infective stages shed from intermediate hosts, few of the above alternatives can be excluded. The least likely to affect the Zoogonus or Stephanostomum distributions would be the third. Neither of these parasites is likely to increase or decrease the chance of further infection. The only other hypothesis which could probably be

excluded is the fifth, since the intensity of neither S. tenue nor Z. lasius varied significantly during sampling.

The fitting of a negative binomial frequency distribution has been used by some authors (Crofton, 1971a; Lester, 1976), to estimate parasite influenced host mortality. The reasoning is that the same factors are influencing infections to all levels of intensity, and thus the characteristics of the distribution should be the same. Crofton, however, noted that in some cases the higher levels of infection contained fewer host individuals than would be predicted. He believed that this was due to parasite induced mortality. Lester (1976) proved in the laboratory that a parasite (Diplostomum adamsi) could cause mortality at the intensities predicted by field data. Mortality was indicated when removal ("truncation") at a certain level of infection led to better agreement with the theoretical distribution. By extension, the fitting of the untruncated negative binomial is an indication that the parasite is not influencing host mortality.

The 1975 data for both S. tenue and Z. lasius were successfully fitted to untruncated negative binomial distributions, indicating a lack of pathogenicity in these species. The value of k (1.68) calculated for S. tenue was greater than the value calculated for Z. lasius (k = 0.429), indicating a higher degree of overdispersion for Zoogonus. According to Crofton's (1971b) model, a value of k less than one indicates that the parasite has little capacity for regulation of its population. The value of k = 1.68 found for S. tenue is a typical value.

The truncated negative binomial fitted to the 1976 Zoogonus lasius data appears to be anomalous. Such a distribution normally is fitted more effectively because mortality has reduced the numbers of heavily

infected hosts. In the case of 1976 Z. lasius, the truncated (at N = 10) distribution fits better because it eliminated a host which had too many parasites. This circumstance probably has no significance beyond its value as a reminder of how far one specimen can vary from the norm. The value of k (0.381) is similar to the value calculated for the same species in the previous year, although Pennycuick (1971 b) has shown that k may vary over the course of the year.

Correlations

A significant difference between two or more groups is one for which there is a 95% certainty that the difference is not due to chance. The meaning of significant is somewhat different when applied to a correlation between two variables (parasite species). In this context it means a 95% certainty that the linear relationship between the variables is not due to chance. The closeness of this relationship, however, is expressed as a correlation coefficient (r). The actual amount of variance which can be attributed to the significant linear regression is equal to r^2. The proportion $1 - r^2$ is the amount unexplained. The level of significance assigned to a correlation coefficient is dependent solely on sample size, and in large samples a significant r may explain less than 10% of the variation between the two sets of numbers. There are degrees of correlation, and a significant correlation coefficient does not imply a close relationship between variables. The advantage of large sample sizes is a better ability to discern low levels of correlation, and thus suggest less than absolute relationships between parasite species. Such relationships could be due to some interaction of the parasites, at some time in their life cycles, or to a mutual reaction to an external stimulus (e.g. temperature).

The only significant correlation which occurred consistently during

the present study was the positive one between Lepocreadium setiferoides and Zoogonus lasius during July, August, and October of 1975; and August and September of 1976. Lepocreadium and Zoogonus share two life cycle characteristics which could account for a positive correlation, i.e. both species utilize Nassarius obsoletus as a first intermediate host and polychaetes as second intermediate hosts. Any circumstance which would influence these common links in their life cycle chains could lead to a positive correlation. If the helminths utilized some polychaete species in common, a fish feeding on this worm would be infected by both parasites. The parasites might use two separate polychaetes which share a habitat, and thus are eaten by flounder at the same time. The possible explanations are numerous.

There is, however, one additional clue to nature of the Lepocreadium - Zoogonus interaction. Although the parasites occurred together all year round, their significant correlations in both 1975 and 1976 coincided with peak Lepocreadium abundance. This suggests that the number of Lepocreadium has an effect on the interaction and therefore that the interaction occurs between the adult flukes in the gut of fish. This is the only place where the number of either species would make a difference. The mechanism for such a synergistic reaction is not known.

There are other explanations for the coincidence of Lepocreadium abundance and a positive Lepocreadium - Zoogonus correlation, and among is pure chance. Unless information is available concerning adults and larvae of both species, intermediate hosts, etc., the correlation of two parasites provides primarily fertile ground for speculation.

PART IV

The Effect of Maintaining Smooth Flounder in the Laboratory Prior to a Parasitological Examination

Introduction

Parasitologists have long recognized that changes in parasite fauna occur when hosts are kept alive in the laboratory for periods of time (Hunninen and Cable, 1942). Only recently, however, have such changes in habitat (MacKenzie and Gibson, 1970) and absolute numbers (Davis and Huffman, 1975; Möller, 1976) been quantified; it is apparent that some changes occur within a relatively short time. Davis and Huffman contended that the greatest loss of helminths occurred between 24 and 48 hrs. after a host was brought into the laboratory, while MacKenzie and Gibson showed that changes in habitat could occur within a day.

Because accurate determinations of parasite numbers and habitats are necessary for many sections of this dissertation, it is imperative that any changes in parasite fauna occurring after a host has been captured be minimized. It is not convenient, however, to post all specimens immediately. To determine the maximum laboratory holding time consistent with acceptable accuracy of results, I systematically examined smooth flounder maintained in the laboratory for up to four days. In addition to ensuring the reliability of the field data, this is the first study to quantify the concurrent changes, in both numbers and position, of all major parasites in a host species.

Materials and Methods

Between June and November, 1975, I collected 0+ age group smooth

flounder from the Lamprey River, Newmarket, New Hampshire (Fig. 1). The fish were seined once per month, and the samples were brought to the laboratory and maintained at 15°C in an aerated container. Starting on the day of capture (day 0), I examined five fish per day for four days. The monthly samples for each of the 5 days were combined in order to increase the sample size per day. Mean and median measures of intensity (number of parasite/fish) were calculated for each parasite for each day. As a result of the non-normality of the data, I tested the changes in intensity between days by the non-parametric Kruskal-Wallis test (Zar, 1974). Any changes in prevalence (percent infestation) as a function of holding time were tested for by the use of contingency tables and subsequent chi-square analysis.

For each of the 30 fish in the five daily samples, I recorded the number of helminths in the anterior, mid, and posterior intestine, as well as the rectum, and calculated the percentages of each parasite infrapopulation in each gut section. These percentages were averaged to give a single set of values for each day. By comparing these data for the 5 days under consideration, I have a measure of any displacement which might occur over time.

Results

The results are presented individually for each of the eight different parasite species found.

Lepocreadium setiferoides (Table 23 and 24)

The mean values show a considerable decrease over time, but due to the variability of the samples, this decline was not statistically significant. The variability of the data was also reflected in the medians, which fluctuated erratically.

TABLE 23

The Mean (± S.D.), Median, and Prevalence of *Lepocreadium setiferoides* as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	87.3 ± 14.9	56.3 ± 79.9	88 ± 177	40.7 ± 69.7	17.9 ± 29.9
Median	17.5	36	39.5	10	8.5
Prevalence	83.4	83.4	82.1	80	96.7

TABLE 24

Percentages of the Population of Lepocreadium setiferoides in the Different Gut Sections as a Function of Lab Holding Time

	Ant. Intest.	Mid Intest.	Post Intest.	Rectum
Day 0	44.2	14.9	22.6	18.3
Day 1	43.1	15.1	35.6	6.1
Day 2	44.4	21.5	24.9	9.3
Day 3	37.4	26.5	16.3	19.8
Day 4	40.7	22.6	21.9	14.8

In contrast to the measures of central tendency, the prevalence of Lepocreadium was constant, and in fact increased somewhat on day 4. This change was not significant.

The mean percentages of the parasite population per gut section changed very little over time.

Zoogonus lasius (Tables 25 and 26)

Like those for Lepocreadium, the values of the mean, median, and prevalence of Zoogonus showed a consistent decline as a function of holding time. Unlike Lepocreadium, this decline was significant. Intensity did not change between days 0 and 1, but decreased significantly on days 2, 3, and 4. A similar trend was evident for prevalence, but in this case only days 3 and 4 were down significantly.

The mean percentages per gut segment for Zoogonus showed little variation over time.

Homalometron pallidum (Tables 27 and 28)

Neither prevalence nor intensity of Homalometron declined significantly during the time in captivity. There was a decrease in the mean value for day 4, but this tendency was less marked than that for Lepocreadium. Since the prevalence of Homalometron was less than 50% on all occasions, the median values for all five daily samples were zero. In cases such as this, the median is an inadequate measure of central tendency.

The parasites, originally concentrated in the anterior intestine, spread out into the posterior intestine and rectum within one day of capture.

Spirurid larva (Tables 29 and 30)

The immediate drop in nematode abundance over time is apparent from the mean values, but the variances are high. As was the case for H. pallidum, the medians are an undesirable measure since they are all

TABLE 25

The Mean (± S.D.), Median, and Prevalence of *Zoogonus lasius*

as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	3 ± 4.8	2 ± 3.2	1.5 ± 3.7	0.8 ± 1.8	0.4 ± 0.5
Median	1.0	1.0	0	0	0
Prevalence	56.7	56.7	35.8	23.3	16.7

TABLE 26

Percentages of the Population of Zoogonus lasius in the Different Gut Sections as a Function of Lab Holding Time

	Ant. Intest	Mid Intest.	Post. Intest.	Rectum
Day 0	0	7.8	24.2	68.1
Day 1	0	0	9.8	91.2
Day 2	0.6	3.8	19.9	75.8
Day 3	0	7.1	16.3	76.5
Day 4	0	4	36	60

TABLE 27

The Mean (± S.D.), Median, and Prevalence of Homalometron pallidum

as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	1.2 ± 2.5	1.1 ± 1.8	1.3 ± 3.0	2.1 ± 5.8	0.4 ± 0.9
Median	0	0	0	0	0
Prevalence	40	36.7	28.6	46.7	23.3

TABLE 28

Percentages of the Population of Homalometron pallidum in the Different Gut Sections as a Function of Lab Holding Time

	Ant. Intest.	Mid Intest.	Post. Intest.	Rectum
Day 0	61	30.7	8.3	0
Day 1	22.7	34.8	34.8	7.5
Day 2	26.3	30.9	29.2	13.6
Day 3	28.1	40.8	16.4	14.8
Day 4	69	31	0	0

TABLE 29

The Mean (± S.D.), Median, and Prevalence of Spirurid Larvae as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	2.1 ± 4.8	0.6 ± 1.2	0.2 ± 0.4	0.7 ± 2.9	0.2 ± 0.4
Median	0	0	0	0	0
Prevalence	40	33.3	17.7	16.7	16.7

TABLE 30

Percentages of the Population of Spirurid larvae in the Different Gut Sections as a Function of Lab Holding Time

	Ant. Intest.	Mid Intest.	Post. Intest.	Rectum
Day 0	64.6	34.7	0.7	0
Day 1	65	32.5	0	2.5
Day 2	60	40	0	0
Day 3	75	5.0	20	0
Day 4	20	4.0	20	20

equal to 0. The large number of zeros in the raw data required that the Kruskal-Wallis test be corrected for ties (Zar, 1975). So corrected, the test showed a significant decrease in abundance over time. Unfortunately, there is no procedure to correct the non parametric multiple range test, and for this reason I cannot precisely determine when the significant changes occur. On the basis of the mean alone, the largest decrease occurred after one day. The prevalence of the nematodes decreased with time, but in this case the first significant decrease is after two days.

The mean percentages of the worm population per gut segment did not change significantly until day 4. The day 4 values are not particularly reliable due to the small number of worms present.

Opecoeloides vitellosus (Tables 31 and 32)

The mean, median, and prevalence values for O. vitellosus were consistently low, and although both intensity and prevalence tended to decrease, in no case was there a significant change.

The O. vitellosus population was originally (day 0) concentrated in the posterior intestine. After one day, the majority were found in the rectum, and this tendency strengthened over time.

Stephanostomum tenue (Table 33)

This species is found as a metacercaria in smooth flounder, and would not be expected to change as a result of lab holding time. The intensity and prevalence values reflected this stability, showing no significant change.

Cryptobia bullocki (Table 34)

The prevalence of this blood flagellate did not change significantly over time.

TABLE 31

The Mean (± S.D.), Median, and Prevalence of *Opecoeloides vitellosus* as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	0.4 ± 0.8	0.3 ± 0.6	0.2 ± 0.4	0.2 ± 0.6	0.1 ± 0.4
Median	0	0	0	0	0
Prevalence	23.3	23.3	21.4	16.7	10

TABLE 32

Percentages of the Population of *Opecoeloides vitellosus* in the Different Gut Sections as a Function of Lab Holding Time

	Ant. Intest.	Mid Intest.	Post. Intest.	Rectum
Day 0	14.3	0	59.6	26.1
Day 1	14.3	14.3	14.3	57.1
Day 2	0	33.4	0	66.7
Day 3	0	0	10	90
Day 4	0	0	0	100

TABLE 33

The Mean (± S.D.), Median, and Prevalence of *Stephanostomum tenue* as Functions of Lab Holding Time

	Day 0	1	2	3	4
Mean (± S.D.)	1.5 ± 1.6	1.3 ± 2.0	1.5 ± 1.3	1.4 ± 1.5	1.7 ± 1.6
Median	1.0	0	1.5	1.0	1.5
Prevalence	63	40	71.5	67	67

Glugea stephani (Table 34)

Like C. bullocki, the prevalence of this protozoan did not change over time.

Conclusion and Discussion

Changes in Abundance

It is not surprising that not all parasites of Liopsetta respond consistently to the host being kept in the laboratory. Some parasites would not be expected to change. Species such as Stephanostomum tenue, Glugea stephani, and Cryptobia bullocki belong to this group. S. tenue is found as a metacercarial resting stage, and while the precise longevity of such larvae is not known, it is longer than four days. This generalization should be true for any larval helminth found outside of the alimentary canal.

G. stephani is a protozoan but also forms resistant resting stages in the flounder. These cysts (containing spores) can remain for considerable periods of time, and their durability would likely be matched by other spore forming, histozoic protozoa (e.g. Myxosporida). The other protozoan parasite of Liopsetta, C. bullocki, does not produce resistant resting stages, but this asexually reproducing form may persist for months in smooth flounder (Strout, 1962). The three species mentioned thus represent three distinct groups of parasites not likely to change in abundance while in captivity. These groups are the encysted helminths (e.g. S. tenue), encysted or spore forming protozoa (e.g. Glugea), and blood protozoa (e.g. Cryptobia).

There were no other representatives of the Phylum Protozoa found during the present study, but experience suggests that some external forms

TABLE 34

The Prevalence of *Cryptobia bullocki* and *Glugea stephani*

as Functions of Lab Holding Time

	Day 0	1	2	3	4
C. bullocki	16.7	16.7	17.7	6.7	10
G. stephani	40	43.3	39.4	43.3	40

such as the trichodinids or other ciliates, flagellates such as Costia, or the dinoflagellate Oodinium, may increase in fish held in the laboratory. Forms such as these have been found to cause epizootics among captive fish (Hoffman, 1967). The possibility of increased abundance over time is also a factor for certain of the Monogenea. Members of the genus Gyrodactylus are known to increase greatly in killifish (Fundulus heteroclitus) maintained in aquaria (W. L. Bullock, pers. comm.)

The group of parasites most liable to show short term changes in the laboratory is the enteric helminths. Since recruitment is not possible for such forms, they must eventually decrease in abundance. The question becomes simply: How quickly does the decrease occur? The evidence in the literature is not conclusive. Möller (1976) was interested in long term changes, and did not specifically report any decreases until 4-5 days after capture. He worked with enteric helminths and reported loss rates of different species, after 42 to 76 days, ranging from 6.5 to 100%. Davis and Huffman (1975), concerned with strictly short term changes, did not separate helminths species, but estimated that the loss of helminths as a group was only 7.3% after 24 hr. This loss, however, increased to 67.3% after 48 hours. Such a rapid loss does not correspond to the work of Möller. Möller's work, moreover, suggested that different helminths respond differently to laboratory holding time.

The results of the present study demonstrate that the enteric helminths do respond differently to their hosts being held in the laboratory. Some species (Zoogonus lasius and the spirurid larvae) decreased significantly, while others (Lepocreadium setiferoides, Homalometron pallidum, and Opecoeloides vitellosus) did not. The difference between groups was not absolute. Although the latter group did not decrease significantly,

the mean intensities went down by 75-80% for both Lepocreadium and Opecoeloides over four days. Because of the great variability of the values (in the case of Lepocreadium), or the low number of infected fish (for Opecoeloides), these numbers were not statistically significant, but they do suggest strongly the rapid loss of enteric parasites by captive fish.

The loss of parasites was particularly apparent for Z. lasius and the spirurid larvae. In the former case, the change in intensity was significant after two days in captivity, and the change in prevalence after three days. The changes in spirurid intensity could not be so precisely defined (for explanation, see Results), but the largest change in mean intensity occurred during the first 24 hr. Spirurid prevalence, on the other hand, did not change significantly until day 3. Prevalence is usually the more conservative measure (see below), but a difference of two days between intensity and prevalence decreases is considerable. My conclusion is that the nematodes decline in abundance at least as fast as Zoogonus.

It is apparent that significant changes in abundance occur in some species very soon after the capture of the host. Consequently, the most accurate reflection of parasite abundance in nature should be made as soon as possible upon return to the laboratory. Practically speaking, however, a statistically significant decrease in parasite intensity was never demonstrated after less than two days holding time, and by extension, the results for day 0 and day 1 were rarely very different. The only exception to this rule was the spirurid larvae, which decreased more rapidly. For all other species, acceptable accuracy for intensity measurement was achieved after holding the host for up to one full day.

The prevalence of enteric helminths was a more conservative measure of abundance change than was intensity. Prevalence did not change significantly for any species in less than two days, and did not show the overall tendency to decrease over time as strongly as did intensity. For these reasons, I conclude that prevalence is not as sensitive to the effects of laboratory holding time. This lack of sensitivity means that an investigation of the prevalence of a parasite need not be so concerned with quickly examining all hosts. This increased flexibility could allow examination of more fish from a given sample, and thus increase sample size, but would be applicable only in the case where the intensity of infection is not in question.

Changes in Habitat Specificity

MacKenzie and Gibson (1970) were among the first workers to precisely describe the habitat specificities for helminths within the gut of a fish and the changes in habitat specificity occurring as the fish were kept in the lab. They used percentages of the total population to describe the changes in position for each species and suggested that changes in distribution occurred after only one day in captivity. The general tendency was for the populations to spread posteriorly.

The results of the present study demonstrate the different degrees of habitat change undergone by different parasite species. Some parasites, like L. setiferoides and Z. lasius, changed little in their distributions over the 4 day study period. This is not surprising in the case of Zoogonus, which is specific for the rectum of smooth flounder. Lepocreadium, on the other hand, occurs in all sections of the intestine and rectum, and yet showed little relative movement over time. This is especially interesting considering the 80% reduction in total population occurring over

the 4 days. The loss of parasites was apparently proportionately equal for all sections of the gut. The stability of the percentages per gut section over time implies a lack of motility on the part of the parasite. This is incongruous when contrasted with the extreme variability of the gut section percentages for individual infections (see Part III).

The final three enteric parasites all showed some degree of change in relative position over time. The case of the spirurid larvae is problematic, since the change from an anteriorly oriented distribution occurred only after the total population had sunk very low. In this situation, the percentages per section are greatly influenced by the position of each worm, and are thus subject to considerable variation. It is not known whether the apparent spreading of the nematodes is an accurate reflection of the population, or merely due to chance.

The change in relative proportions per gut segment was more distinct for H. pallidum and O. vitellosus. In both cases the major change in distribution occurred after one day of captivity, and in both cases it involved a shift to the more posterior regions of the gut. These data agree with the findings of MacKenzie and Gibson (1970). The changes, especially for H. pallidum, involve larger numbers of parasites than was the case for the spirurid larvae. The distributions, however, are still subject to the criticism that too few worms were involved in describing them.

The reason for changes in parasite distribution are poorly known. MacKenzie and Gibson (1970) showed that Podocotyle sp. responded to the presence of liver bile, and Croll (1976) has shown that some nematodes orient to food in the gut. The most apparent change which occurs in the smooth flounder gut during their first day in captivity is the loss of

food. It is probably not coincidental that this time period corresponds to the most dramatic changes in H. pallidum and O. vitellosus distribution. Why these species would respond to changes in gut content, and some others would not, is not known. MacKenzie and Gibson suggested that part of the answer lies in the different motilities of the different parasites. They hypothesized that the mobile species responded more readily.

To accurately determine parasite habitat specificities in the gut, my results indicate that generally no fish should be posted more than one day after being captured. This one day grace period corresponds to the maximum holding time allowable for intensity investigations.

PART V

The Parasites of Smooth Flounder, Liopsetta putnami (Gill), at two Sites in the Great Bay estuary, New Hampshire

Introduction

Within a host species, especially one from a locally defined area, the evolutionary adaptations to parasitism among individuals can be considered to be the same. Therefore, any differences in parasite fauna are due to ecological factors, i.e. to differences in opportunities for contact with parasites. Such differences can occur among individuals from the same habitat. There are, for example, individual variations in food preference leading to differential contact with intermediate hosts. Furthermore, Crofton (1971a) has emphasized the advantage of processes of infection which produce overdispersed (high variance) distributions of parasites within a host population.

Notwithstanding individual differences, however, any habitat provides a certain spectrum of opportunities for parasitic infection, and different habitats provide different spectra. The host population as a whole, therefore, acquires a particular array of parasites, and this assemblage can be used to characterize the habitat and compare it to others. Any movement of a host through different habitats should be reflected in its parasite fauna. This principle has been utilized to "tag" the long range migrations of anadromous fish (Margolis, 1963. 1965; Konovalov and Konovalova, 1969; Pippy, 1969). The study of more local fish movements has been hindered by the homogeneity of local environments. Estuaries, however, are anything but homogeneous and lend themselves to such studies. The investigations of local mixing and movements by

MacKenzie (1968), Gibson (1972) and Olson and Pratt (1973) were all carried out with estuarine fish species. In addition to such host-related information, the study of parasite variation within an estuary is an interesting example of how different the parasites of a single host species can be.

The biology of the smooth flounder is not well known. In the Great Bay estuary it inhabits areas ranging from near oceanic salinity to the uppermost reaches of brackish water. The extent of interaction of fishes from different areas of the estuary is not known. The free living communities (i.e. prospective intermediate hosts) associated with the flounder vary greatly, and should give rise to different parasite assemblages. If the flounder show such differences, the fish are not mixing freely. Such mixing would negate the effects of a heterogeneous environment, and would lead to a homogeneous parasite fauna. Mixing obviously need not lead to complete homogeneity, but unfortunately, degrees of interaction are difficult to resolve. It is often possible, however, to use known life cycle and intermediate host distribution data to help clarify such situations. The use of more than one parasite species is often helpful in this regard, since their variable distributions provide more than one way of analyzing a given movement. The most valuable parasites for this purpose are those with limited ranges.

A parasite assemblage can be quantified not only as an enumeration of species, but also by diversity indices. Davis and Huffman (1975) stated that such indices can provide an estimate of the diversity of the local free living community, and such diversity indices have been used as a measure of environmental quality. In an estuary, the natural variation of habitats precludes any such interpretation. It would be interesting,

however, to attempt to correlate the diversity of both parasite and free-living communities, and the estuary provides an ideal area for such a study.

The extent of variability of flounder parasites within the Great Bay estuary is thus of interest both as a measure of movement of the fish themselves and for its possible correlation to similar variation in the free living community. It was decided, therefore, to study this variation with a detailed comparison of flounder parasites from two dissimilar areas of the estuary. The amount of variation between these sites could provide a rough measure of the mixing (or lack thereof) of smooth flounder from the two areas. Parasite diversity indices from each site could also be compared to observations of the free living community. Since such indices are dependent on the number of species present, measures of evenness should also be calculated.

Materials and Methods

Collections for this study were made as part of a larger scale study of smooth flounder parasites. During July, August, and September, 1974 and July, August, September and October, 1975, 0+ age group smooth flounder were seined from the Lamprey River and General Sullivan Bridge (Trichy's Cove) sites indicated on Figure 1. Proportionately equal numbers of fish were caught at each site in each month, and the monthly samples from each site were not separated by more than three days. Water temperature and salinity were recorded for each site at the time of collection. In 1974, a total of 32 fish were collected from the Lamprey River and 24 from the area of the General Sullivan Bridge. In 1975, 40 fish were collected from the Lamprey and 42 from the Sullivan Bridge site.

The fish were brought to the laboratory in buckets, measured, and necropsied within 36 hours of capture. All protozoan and metazoan parasites were identified and counted. The 1974 and 1975 collections from each site were compared separately, differences in fish length being tested by a t-test and differences in intensity of infection (mean number per fish) with each parasite by the Mann-Whitney test. The non-parametric Mann-Whitney test was used since the frequency distributions of numbers of parasites per fish were overdispersed. Differences in prevalence of infection (percent infestation of the fish population) with a particular parasite were tested with 2 X 2 contingency tables and subsequent chi-square analysis.

The simplest measure of diversity consists of a simple compilation of the number of species, s. Further estimation of the parasite community diversity was made by calculation of the Shannon-Wiener index ($H' = \Sigma\ p_i\ \ln\ p_i$) as described by Hutcheson (1970) (see Appendix I) for both sites for both years. Also following Hutcheson, t-tests were made to compare diversity indices for both sites for 1974, 1975 and the totals for the two years. Evenness (= equitability) was calculated according to the recommendations of Pielou (1966, 1969, 1974). Both diversity indices and evenness can be calculated only from parasite species whose number per fish can be counted. Therefore, only metazoan species were used for this purpose.

Results

The physical and biotic characteristics of the collecting sites are considerably different. The 1974 and 1975 temperature and salinity data for these habitats are given in Table 35.

TABLE 35

Water temperature (°C) and salinity (ppt) from the Lamprey River (L.R.) and General Sullivan Bridge (G.S.B.)

		Temperature				Salinity			
1974		July	Aug.	Sept.	Oct.	July	Aug.	Sept.	Oct.
	L.R.	24	22.5	19	-	22	30	15	-
	G.S.B.	16	16	17	-	31	32	30	-
1975									
	L.R.	28	21	18	11	15	22	8	2
	G.S.B.	19	21	16	11	30	32	32	30

The upper estuary (Lamprey River) is a much more extreme habitat in terms of both temperature and salinity. It reaches very high temperatures during mid summer, and the reduced fresh water flow leads to almost oceanic salinities which decline rapidly with autumn rains. In contrast, the General Sullivan Bridge site showed little fluctuation in salinity during the study period. The temperature variation was also more conservative.

The Lamprey River collecting area is shown in Figure 4. It is dominated by a soft mud substrate, bounded in most places by a narrow border of Spartina spp. There is a small outcropping of rock near mid tide level, but no macro-algae are present. The General Sullivan Bridge site, shown in Figure 5, is more varied, ranging from soft mud to a gravel and rock beach above mid tide level. There are numerous large rocks present, and these support heavy algal communities.

The parasites identified from the two collection sites are listed in Table 35. The species are divided into protozoan and metazoan groups, and the members of each group are listed in approximate order of abundance.

The final four species on the list of metazoa from the Lamprey River were represented by a single specimen, and L. confusus was found only twice. All other metazoa from the Lamprey River were found more commonly. At the General Sullivan Bridge Trichodina sp. was found on only one fish, and Cryptobia bullocki was uncommon at both sites. When the occurrence of these rare species is taken into account, the lists of parasites are quite similar. Nine species (marked on Table 3 with an asterisk) were found on smooth flounder from both locations. The only exceptions not previously mentioned are A. laticauda from the Lamprey River and C. lingua from the General Sullivan Bridge site. The branchiuran is

TABLE 36

Parasites from 0 age group smooth flounder at two sites in the Great Bay estuary, N.H. (Species common to both sites are marked by an asterisk).

Lamprey River (n = 72)	General Sullivan Bridge Site (n = 66)
Metazoa	Metazoa
*1. Lepocreadium setiferoides	*1. Lepocreadium setiferoides
*2. Zoogonus lasius	2. Cryptocolyle lingua
*3. Stephanostomum tenue	*3. Zoogonus lasius
*4. Homalometron pallidum	*4. Homalometron pallidum
*5. Spirurid larva	*5. Stephanostomum tenue
*6. Opecocloides vitellosus	*6. Opecoeloides vitellosus
7. Argulus laticauda	*7. Spirurid larva
8. Lecithaster confusus	
9. Tubulovesicula pinquis	Protozoa
10. Gynaecotyla adunca	
11. unidentified monogenean (imm.)	*8. Glugea stephani
12. Proteocephalid (immature)	*9. Unidentified sporozoan 1
	*10. Cryptobia bullocki
Protozoa	11. Trichodina sp.
*13. Glugea stephani	
*14. Unidentified sporozoan 1	
*15. Cryptobia bullocki	

not common enough to be important as a tag. C. lingua, however, is very abundant at the Newington site, and its absence is conspicuous at the Lamprey River.

Although the species present are similar at the two sites, there were considerable differences in prevalence and intensity of infection. The levels of parasite intensity and prevalence (for all parasites except the singly occurring species) are given in Tables 37 and 38. Within each study period, infections found to be significantly greater (at the 95% level) than at the other site are marked with an asterisk.

The most dramatic difference was the consistent high intensity and prevalence of C. lingua at the General Sullivan Bridge, and the complete lack of this species from 0 age group fish from the Lamprey River. The only other difference which held for both 1974 and 1975 was the higher intensity of S. tenue infections from the Lamprey River. Prevalence of the parasite was also greater at the Lamprey, but not significantly so.

A similar situation can be seen for the unidentified sporozoan 1 and Myxobilatus sp., both of which were significantly more prevalent at the General Sullivan Bridge site in 1975. The survey did not include these species in 1974.

There were two instances in which the intensity and prevalence were both significantly greater at one site for one year only. In 1974, infections of Z. lasius were higher at the General Sullivan Bridge, while in 1975 there was no difference. In 1975, the spirurid nematodes were found more frequently at the Lamprey River. There is also the situation where in 1974, L. setiferoides showed a significantly higher intensity, but not prevalence, at the Newington site. In 1975 the same area showed a higher prevalence, but not intensity of L. setiferoides infection.

TABLE 37

Mean Intensity of Infection at two sites - 1974 and 1975

(L.R. = Lamprey River, G.S.B. = General Sullivan Bridge)

(Significant differences between the sites are marked by an asterisk)

	1974		1975	
	L.R. (n=32)	G.S.B. (n=24)	L.R. (n=40)	G.S.B. (n=42)
L. setiferoides	13.8	56.9*	95.1	56
C. lingua	0	12.2*	0	7.8*
Z. lasius	0.3	2.8*	2.4	3.7
H. pallidum	0.2	6.3*	1.2*	0.2
S. tenue	0.7*	0.1	1.5*	0.4
spirurid	0.3	0.2	1.2*	0.1
O. vitellosus	0.1	<.1	0.4	0.2
L. confusus	0.1	0	0	0
A. laticauda	0.1	0	0.1	0

TABLE 38

Prevalence of Infection at two sites, 1974 and 1975

(L.R. = Lamprey River, G.S.B. = General Sullivan Bridge)

(Significant differences marked by an asterisk)

	1974		1975	
	L.R. (n=32)	G.S.B. (n=24)	L.R. (n=40)	G.S.B. (n=42)
L. setiferoides	87.5	100	87.5	100*
C. lingua	0	87.5*	0	83.3*
Z. lasius	12.5	70.8*	52.5	61.9*
H. pallidum	15.6	87.5*	40*	16.7
S. tenue	34.4	12.5	47.5	30
spirurid	25	12.5	35*	7.1
O. vitellosus	9.4	4.2	30	19
A. laticauda	3.1	0	7.5	0
L. confusus	6.3	0	0	0
G. stephani	28.1	25	45	28.6
Myxobilatus sp.	-	-	0	11.9*
unident. sporo. 1	-	-	27.5	59.5*
C. bullocki	3.1	0	7.5	2.4

The final significant difference between the Lamprey River and General Sullivan Bridge sites was an unusual one. The pattern of occurrence of H. pallidum reversed between 1974 and 1975. In 1974 the trematode was more common at the Bridge site, and in 1975 at the Lamprey River. This reversal was valid for both prevalence and intensity of infection, and H. pallidum was the only species showing such a change.

The diversity indices and evenness values calculated for the two parasite-mixes are given in Table 39.

For both 1974, 1975, and the combined sample, the parasite diversity was found to be significantly greater at the General Sullivan Bridge than at the Lamprey River, and the evenness values showed a similar pattern.

In addition to the differences in parasite fauna, 0+ age group smooth flounder differed somewhat in size. The average lengths of the fish studied were 8.2 (1974) and 9.0 (1975) cm at the General Sullivan Bridge site, and 7.8 (1974) and 8.1 (1975) cm at the Lamprey River. The greater size of the Sullivan Bridge site specimens was statistically significant in 1975.

Discussion

To be useful as a biological tag, a parasite species must be relatively common. The five species (T. pinquis, G. adunca, unidentified monogenean, immature proteocephalid, Trichodina sp.) which were found only once are of little value by this axiom. Lecithaster confusus (2 specimens) and Argulus laticauda (5 specimens) are also not definitive. Taken collectively, these species do suggest that the level of interaction between 0 age group smooth flounder from the two areas is low.

TABLE 39

Diversity Indices (H') and Evenness (J') calculated from the metazoan parasite communities at the Lamprey River (L.R.) and General Sullivan Bridge (G.S.B.) in 1974 and 1975. (Significant differences in H' are marked with an asterisk)

		L.R.	G.S.B.
1974	H'	.3724 nats	.8441 nats *
	J'	.1695	.4338
1975	H'	.3528 nats	.6429 nats *
	J'	.1531	.3304
Total	H'	.3497 nats	.7530 nats *
	J'	.1407	.3869

The two species which provide the strongest evidence for this are Myxobilatus sp. and Cryptocotyle lingua. The absence of both parasites from the Lamprey River is a good indiciation that it receives no recruits from the General Sullivan Bridge site. Since there is no common parasite found only at the Newmarket site, I cannot make the converse statement. This is one of the limitations of purely parasitological methods, and does not necessarily imply any mixing of stocks. A lack of movement by 0+ age group fish would correspond with the findings of Pearcy (1962) for winter flounder.

By utilizing our knowledge of the life cycle of C. lingua and of the local distribution of its intermediate host, we can explain both the discontinuous distribution of the parasite and to further refine our conclusions about host movements. C. lingua matures in gulls, and uses littorine snails (Littorina littorea, L. obtusata) as first intermediate hosts. Smooth flounder (and many other fish) serve as the second intermediate host. Although there is no lack of seagulls at the Lamprey River, the life cycle cannot be completed there due to the absence of the proper snail host. Both of the necessary snails are present at the General Sullivan Bridge area, although their upstream range is only to the region of Adams Point in Durham and Fabyan Point in South Newington (see Figure 1). None of the youngest smooth flounder moved from these positions to the Lamprey River. Small numbers of C. lingua have been found in older Lamprey River flounder. This serves as an indication that at least some of these fish have travelled as far as Adams Point or Fabyan Point. Pearcy (1962) has pointed out that older juveniles and adults of the winter flounder are less sedentary than the 0+ age group fish, a conclusion that appears to be valid for smooth flounder also.

The C. lingua and Myxobilatus sp. data are most valuable because they are absolute, and indicate that no upstream movements of flounders occurs during their first summer of life. The other parasite species are less conclusive because their differences are less absolute. Their occurrence can, however, provide information. While there is no proof (from parasitological data) that downstream movement of 0 age group flounder does not occur, the number of significant differences in intensity and prevalence of infection among parasite species argues against it. Such differences would not occur if large scale migration were taking place. The results, however, don't preclude the movement of some fish. In order to answer this question, it would be necessary to use more traditional methods of tagging fish from the upper estuary.

Given the differences between the collecting sites, it is not unexpected that some parasites were able to complete their life cycles more successfully at one site than the other. Some results, however, were intriguing. For example, the most common species in either habitat is Lepocreadium setiferoides. The tendency seems to be for this trematode to be more common at the Sullivan Bridge. The high mean intensity for the Lamprey River in 1975 is due to a few heavily infected fish, and the difference is not significant. L. setiferoides is unusual because although it reaches very high intensity infections, very few of these worms become gravid. Of the 4295 worms found in Lamprey River smooth flounder during 1974-75, only 22 were gravid. During the same period, 98 of 3973 worms were gravid at the General Sullivan Bridge. This is a significant difference ($X^2 = 55.1$, $df = 1$, $P < .005$). Magendantz (1969) also noticed the low proportion of gravid L. setiferoides in L. putnami, and suggested that smooth flounder

may not be the most suitable definitive host for this worm. The present results indicate that habitat may also play a role in the maturation of this species. No other trematode showed a difference in maturity between the two collection areas.

The case of Homalometron pallidum is unusual because of the complete reversal of its occurrence between 1974 and 1975. The population decline at the General Sullivan Bridge and simultaneous increase at the Lamprey River are not easily explained. The environmental parameters don't appear to have changed enough to precipitate such a drastic alteration. The complicated life cycles of digenes like H. pallidum, however, allow for numeroud interactions between different intermediate hosts and the environment. At present, there is simply not enough information to explain the situation.

A final somewhat unexpected finding is that Stephanostomum tenue metacercariae are more abundant in Lamprey River flounder than in those from the General Sullivan Bridge. According to Martin (1939), the definitive host is the striped bass and the first intermediate host is Nassarius obsoletus. The flounder and snail hosts are abundant in both areas; however, the bass are far more common in the more seaward areas of the estuary. The question becomes simply, why are the trematodes more common in the upper estuary? No definite answer is available, but one possibility is that S. tenue may use another definitive host, such as the white perch (Morone americana), which is congeneric with striped bass and very common in the Lamprey River. Limited examinations of Lamprey River white perch have not revealed any S. tenue infections.

As suggested by the descriptions of the Lamprey River and General Sullivan Bridge sites, the latter area is more heterogeneous in terms of

available habitats and almost certainly supports a more diverse free living community. The task of quantifying this diversity (such as by diversity indices) was beyond the scope of this work, but the superficial differences are dramatic.

The metazoan parasite diversity indices calculated for smooth flounder from the two sites reflect the probable differences in community diversity. In all instances the General Sullivan Bridge site showed significantly greater diversity, despite the slightly greater number of species at the Lamprey River. The primary reason for the low diversity values at the Lamprey River is the extreme dominance of L. setiferoides at this site. The apparent correlation between the parasite and free living community diversity supports the contention of Davis and Huffman (1975), that parasite data might be used as a substitute for community diversity in evaluating water quality.

In calculating evenness, the number of metazoan parasite species in the sample, s, was used as an approximation of the total number of species in the community (usually abbreviated s*). The assumption seems justified in this case because of the relatively limited nature of any parasite fauna, as opposed to the much more complex composition of the free living community. As a result of the possible bias involved in estimating s*, Peet (1975) suggested the necessity for equal sample sizes when calculating evenness from different environments. Although the Lamprey River and General Sullivan Bridge samples are relatively close in number, the more self-contained nature of parasite populations would seem to minimize this problem.

Conclusion

In agreement with earlier workers (MacKenzie, 1968; Wickens and

Macfarlane, 1973; Gibson, 1972; Olson and Pratt, 1973), it was shown that a relatively small number of parasite species, i.e. C. lingua and Myxobilatus sp., are of use as biological indicators of actual movement or mixing of stocks. Familiarity with all parasites is necessary, however, before these species can be identified. As is typical of parasite based studies, not all of our questions can be answered.

The collecting sites can be separated not only on the basis of flounder parasite species present, but also by diversity indices. Differences in these indices serve as a confirmation of the results of our actual parasite survey; namely that the parasite-mix for smooth flounder differs at the Lamprey River and General Sullivan Bridge. It is uncertain whether the indices provide useful information in their own right. There is an apparent positive correlation between parasite and free-living community diversity, but the precise relationship has never been demonstrated. The correlation may be an intuitively correct one, but there is a need to more quantitatively investigate it.

There are three aspects of parasite diversity which would be interesting to study. These points are to a large degree integrated with each other. The first concerns the use of parasite diversity to measure environmental quality. This technique depends on the consistent correlation of free-living and parasite diversities. If valid, it would greatly simplify the calculation of meaningful diversity indices.

The second point concerns the variability of parasite diversity indices calculated from different hosts from the same environment. This applies itself to the question of how accurately do different hosts represent their environment. It would seem that the most favorable host would be an opportunistic feeder likely to "sample" the broadest spectrum

of the community. Davis and Huffman (1975) demonstrated a consistent difference between the helminth diversities of Gambusia affinis and G. geiseri in the San Marcos River. Differences of this sort would seem to indicate the necessity for utilizing the same host species to sample different habitats.

Finally, it would be interesting to determine if parasite diversity indices alone could be used to separate stocks of fish. We have seen that frequently only one or two species are valuable as "biological tags" of movement or mixing. If such species were not present, the study of parasites would be of little use. If, however, it were possible to accurately separate stocks on the basis of their total parasite fauna, the utility of such data is enhanced.

PART VI

A Comparison of the Parasites of Smooth Flounder, Liopsetta putnami, and Winter Flounder, Pseudopleuronectes americanus, in the Great Bay estuary, New Hampshire

Smooth flounder and winter flounder are members of the Pleuronectidae. Juveniles of both species are found in shallow water at the General Sullivan Bridge, Newington, New Hampshire. The species are morphologically similar (e.g. right eyed and small-mouthed) and preliminary observations have noted a similarity in diet. Several studies (Linton, 1921; Pearcy, 1962; Richards, 1963; Frame, 1974) have demonstrated the opportunistic nature of feeding in juvenile winter flounder, and smooth flounder juveniles share this characteristic. Pearcy (1962) has shown that winter flounder are very sedentary during their first summer of life, and parasitological evidence suggests a similar situation for Liopsetta (see Part V, this dissertation). The presence of two such similar species in a single habitat raises questions concerning the competitive exclusion principle (Hardin, 1960); however, the actual extent of competition is not known.

Since smooth and winter flounder are so similar in morphology, diet, and habitat, we might expect their parasites to be much alike. By comparing the parasite faunas of smooth and winter flounder at the General Sullivan Bridge, it is possible to gain insight regarding the host specificity of certain parasites. Such species would be primarily those with a direct life cycle (e.g. Monogenea and Myxosporidea), or the stages of a more complex cycle which actively infect a host (e.g. cercariae). These parasites would theoretically be equally likely to infect two

demersal fish species from the same habitat. Those parasites which are passively ingested can also provide information, to an extent, concerning host specificity and also about the diets of the flounder species. Such dietary information can provide a measure of how directly the two species compete.

In the previous section, I raised a question concerning the relationship of parasite diversity indices from different hosts in the same habitat. The occurrence of L. putnami and P. americanus at the General Sullivan Bridge presents an opportunity to compare the indices from two similar "samplers" of the same environment. This information is useful in order to determine how consistently the different hosts will reflect their habitat.

Materials and Methods

As a part of a larger parasite survey, collections of age-group 0 smooth and winter flounder were made during three separate time periods in 1974-1975. Proportionately equal numbers of each host species were seined at intervals during these periods. The first collections were during July and August, 1974, when 11 winter and 16 smooth flounder were caught. Twelve winter and seven smooth flounder of the 1974 year class were also collected between March and May, 1975. At this time they were technically yearlings, but were still the youngest fish available since the 1975 class had not yet metamorphosed. The 1975 year class flounder were collected between July and October, 1975. During this period, 11 winter and 42 smooth flounder were seined. Upon collection, the flounder were brought to the laboratory and maintained in aerated buckets until they were measured and necropsied within 36 hours of capture.

All parasites were identified and counted. Since the relative maturity of a helminth is known to vary in different hosts, the presence of any eggs was noted.

Intensity and prevalence of all parasite infections were calculated for each collection period. For parasites found in both species, differences in intensity were tested using the Mann-Whitney test. Differences in prevalence were tested with 2 X 2 contingency tables and subsequent chi-square analysis.

Estimates of parasite diversity were made by calculation of the Shannon-Wiener Index ($H = -\Sigma\ p_i\ \ln\ p_i$) as described by Hutcheson (1970) (see Appendix I) for all three collecting periods. Also following Hutcheson, t-tests were done to test the differences between these indices for the different hosts species. Evenness (= equitability) was calculated for each sample according to Pielou (1974). Both diversity indices and evenness were calculated using metazoan parasites, since only these can be counted.

Results

The species of parasites found in smooth and winter flounder from the General Sullivan Bridge are recorded in Table 40. This table includes species found during all three collecting periods.

The parasite species present are similar in L. putnami and P. americanus. The only species not common to both hosts were Protancyrocephaloides liopsettae, Opecoeloides vitellosus, and Trichodina sp. among the parasites of Liopsetta and Ascarophis and Stephanostomum baccatum from winter flounder. Of these species, O. vitellosus and Trichodina sp. were so rare that they are of little use as indicators of host specificity or diet.

TABLE 40

Parasites of Smooth Flounder (*Liopsetta putnami*) and Winter Flounder (*Pseudopleuronectes americanus*) Collected from the General Sullivan Bridge (1974-1975)

L. putnami (n = 65)	*P. americanus* (n = 34)
Metazoa	Metazoa
1. *Lepocreadium setiferoides*	1. *L. setiferoides*
2. *Homalometron pallidum*	2. *H. pallidum*
3. *Cryptocotyle lingua*	3. *C. lingua*
4. *Zoogonus lasius*	4. *Z. lasius*
5. *Stephanostomum tenue*	5. *S. tenue*
6. *Protancyrocephaloides liopsettae*	6. *Stephanostomum baccatum*
7. *Opecoeloides vitellosus*	7. *Ascarophis* sp.
8. Spirurid larva	8. Spirurid larva
Protozoa	Protozoa
9. *Glugea stephani*	9. *G. stephani*
10. *Cryptobia bullocki*	10. *C. bullocki*
11. *Myxobilatus* sp.	11. *Myxobilatus* sp.
12. Unidentified Sporozoan 1	12. Unidentified Sporozoan 1
13. Unidentified Sporozoan 2	13. Unidentified Sporozoan 2
14. *Trichodina* sp.	

The prevalence and mean intensity of infection for the various parasite species are summarized in Tables 41 and 42. These values are given separately for each sampling period.

The ratio of gravid (egg-bearing) to non-gravid forms was relatively constant for most helminths found in both flounder hosts. In the case of L. setiferoides, however, the proportion gravid was significantly greater in P. americanus than it was in L. putnami. In the summer of 1974, 4.4% of the L. setiferoides were gravid in winter flounder, while only 1.1% were so developed in smooth flounder. The difference was even more dramatic in the summer of 1975, when the percentage gravid was 25.7% in P. americanus and 4.1% in L. putnami. In both years the difference in percent gravid was statistically significant at the 95% level. There was no difference in maturity for the spring 1975 sampling period since no mature worms were found.

The diversity indices and evenness values calculated for the parasites of the two flounder species are given in Table 43.

There was no significant difference between the diversity or evenness values for the first two study periods. However, the diversity of the winter flounder helminths was much greater in the summer of 1975.

Discussion

Different species, by definition, have different evolutionary histories. For this reason the evolutionary factors which partially determine the parasite fauna of the species, i.e. the physiological adaptations which allow parasite and host to live together, will also be different. Thus, even if diet, habitat, and other ecological factors which determine opportunity for contact with parasites are the same, the

TABLE 41

Prevalence of Parasite Infections for Smooth Flounder (*Liopsetta putnami*) and Winter Flounder (*Pseudopleuronectes americanus*) at the General Sullivan Bridge (1974-1975). Significant differences between host species are marked by an asterisk.

	July - August 1974		March - May 1975		July-October 1975	
	Smooth n = 16	Winter n = 11	Smooth n = 7	Winter n = 12	Smooth n = 42	Winter n = 11
L. setiferoides	100	100	87.5	91.7	100*	63.6
H. pallidum	100	100	0	0	16.7	72.7*
C. lingua	93.8*	63.6	42.9	75	83.3	72.7
Z. lasius	75*	9.1	57.1*	8.3	61.9*	9.1
S. tenue	6.3	0	42.9	16.7	28.6*	0
S. baccatum	0	0	0	25	0	0
O. vitellosus	6.3	0	0	0	19	0
P. liopsettae	0	0	85.7*	0	0	0
Ascarophis	0	0	0	8.3	0	36.4*
Spirurid	25	0	0	8.3	7.1	0
G. stephani	0	0	0	41.7*	26.2	36.4
C. bullocki	0	0	85.7	58.3	2.4	0
Myxobilatus sp.	0	0	0	0	7.1	63.6*
unident. sporo. 1	-	-	0	0	59.5	72.7
unident. sporo. 2	-	-	28.6	41.7	0	18.2
Trichodina sp.	0	0	14.3	0	2.4	0

TABLE 42

Mean Intensity of Infections of Smooth Flounder (Liopsetta putnami) and Winter Flounder (Pseudopleuronectes americanus) at the General Sullivan Bridge (1974-1975). Significant differences between host species are marked by an asterisk.

	July - August 1974		March - May 1975		July - October 1975	
	Smooth n = 16	Winter n = 11	Smooth n = 7	Winter n = 12	Smooth n = 42	Winter n = 11
L. setiferoides	49.9*	12.5	16.7	13.4	54.8*	10.1
H. pallidum	8.2	32.9*	0	0	.2	5.6*
C. lingua	10.9	3.8	3.4	16.7*	7.8	6.7
Z. lasius	2.9	0.1	0.9*	0.1	3.7*	0.1
S. tenue	0.1	0	0.7	0.2	0.4	0
S. baccatum	0	0	0	4.5*	0	0
O. vitellosus	0.1	0	0	0	0.2	0
P. liopsettae	0	0	6.1*	0	0	0
Ascarophis sp.	0	0	0	0.1	0	1.6*
Spirurid	0.3	0	0	0.1	0.1	0

TABLE 43

Diversity Indices (H') and Evenness (J') calculated for metazoan parasites of smooth flounder (Liopsetta putnami) and winter flounder (Pseudopleuronectes americanus) from the General Sullivan Bridge (1974-1975). Significantly greater values are marked with an asterisk.

	Smooth	Winter
July-August 1974	n = 16	n = 11
H'	.9489 nats	.8240 nats
J'	.4876	.5943
March-May 1975	n = 7	n = 12
H'	1.088 nats	1.046 nats
J'	.6760	.5377
July-October 1975	n = 42	n = 11
H'	.6429 nats	1.2556 nats *
J'	.3304	.7801

parasite faunas of different species should be somewhat different. These evolutionarily determined differences between hosts are an important component of host specificity (Margolis, 1965).

Although the lists of parasites of the two flounder species are similar, there are differences which provide examples of host specificity. Since detailed dietary information is not available, only parasites which actively infect their host are reliable indicators of this phenomenon. Of the common species which fit this criterion, the most specific is the monogenean Protancyrocephaloides liopsettae, which is very abundant on smooth flounder in the spring, but has never been found on any other host. Specificity of this degree indicates a finely tuned interaction and is a sign of a long standing relationship between parasite and host. Monogenetic trematdoes as a group are very host specific (Hargis, 1957). Hargis stated that this specificity "may be either physiological and genetic and/or ecological in basis...". In the present case, the physiological and genetic (i.e. evolutionary) factors appear to be preeminent, since ecological differences are not apparent.

Stephanostomum tenue and Myxobilatus sp. are parasite species for which the specificity is not absolute. Both, however, demonstrate a significant difference in occurrence between smooth and winter flounder. Although S. tenue is found as a metacercaria in both hosts, it is more common in smooth flounder. The cercariae either infect this host species more readily, or alternatvely, survive better in them after infection. Further experimentation would be necessary to separate these hypotheses. The basis for the interspecific difference, however, is almost definitely physiological.

The case of Myxobilatus is even more clear cut, since infection

probably occurs by incidental ingestion of spores. Granting that the opportunity to ingest these spores would be similar for two flounder from the same habitat, any differences in infection rate must be physiologically derived. The increased incidence of the parasite in winter flounder is such a case. The specificity of Myxobilatus (and S. tenue) is not so exact as that of P. liopsettae, but this does not necessarily imply a younger or less highly evolved relationship with their hosts.

The final actively infectious parasite to be considered is Cryptocotyle lingua. This species is interesting because of the changes in relative occurrence for smooth and winter flounder over the three sampling periods. These differences preclude any conclusions about the relative specificity of C. lingua for the two flounder species. Since it occurs in many fish species, the metacercaria of C. lingua is considered to be very non-specific. It is possible to explain the reversal in C. lingua occurrence between 1974 and spring 1975 on the basis of changes in population structure following winter migration. This argument, however, cannot explain the lack of difference between smooth and winter flounders for summer 1975. Given the wide occurrence of C. lingua in many coastal fish, the considerable difference in parasitism between flounder species seen in 1974 may represent a statistical fluke.

If a parasite species infects its final host passively, i.e. by means of an intermediate host, we cannot definitively tell whether differences in its occurrence in two hosts are due to host dietary differences (and thus differential exposure to intermediate hosts) or to physiologically mediated host specificity. This is the situation for

Ascarophis sp., Zoogonus lasius, Homalometron pallidum, and Lepocreadium setiferoides, all of which show consistent difference in occurrence between smooth and winter flounder. For the first three species, there is no solution to this problem. The situation is, in fact, even more complicated since the trematodes mentioned all occur (and even mature) in several host species other than flounder. For L. setiferoides, however, the differential maturity of the trematode infections provides an additional clue. Since this trematode matures more successfully in winter flounder, it seems unlikely that physiological host specificity would be the cause for the significantly lower levels of infection in this host. A more likely answer is that while Lepocreadium more successfully matures in, and is thus more specific for, P. americanus, a different diet leads to higher intensity infections in L. putnami. In Liopsetta, the worms can live but do not readily mature. This differential maturation of L. setiferoides in smooth and winter flounder was also noticed by Magendantz (1969). The occurrence of Lepocreadium thus provides evidence not only for the host specificity of the trematode but also for a difference in diet for the two hosts, and thus a reduction of competition. The data suggest that smooth flounder consume greater numbers of small polychaetes (such as Polydora ligni) than winter flounder, and as a result are infected with greater numbers of L. setiferoides in the intestine, but few mature worms. This evidence for a somewhat different diet in smooth and winter flounder strengthens the case against using passively acquired parasites as indicators of host specificity.

A difference in occurrence that has not been previously mentioned is the presence of Stephanostomum baccatum in winter flounder during spring, 1975. Although no S. baccatum were found in smooth flounder,

this is not considered to be the result of host specificity. The first intermediate hosts of S. baccatum are Buccinum undatum and Neptunea decemcostata (Wolfgang, 1955). There are marine snails, and neither is found at the General Sullivan Bridge. The S. baccatum infections in yearling winter flounder indicate that these fish spent their first winter either in the ocean or close to it. Such a finding is in accord with Pearcy (1962), who found the first year juveniles over-wintered in the more seaward areas of the estuary. S. baccatum thus serves in this case as a "tag" to help understand winter flounder movements. Whether these S. baccatum infected juveniles actually originated at and returned to the General Sullivan Bridge is not known. It is certain, however, that young fish with marine exposure moved into the area in spring, 1975.

There is no handy tag such as S. baccatum to help illucidate smooth flounder movements in the General Sullivan Bridge area. The absence of S. baccatum in the smooth flounder would, however, seem to preclude any seaward movement and subsequent return. Wolfgang (1955) and Ronald (1960) have indicated that L. putnami can be infected with S. baccatum if exposed to the cercariae.

The results of diversity indices calculated for smooth and winter flounder parasites are inconclusive. There is remarkably good agreement between the species for the first two collecting periods. This is somewhat incongruous since the winter flounder present at the General Sullivan Bridge in the spring show good evidence (e.g. the presence of S. baccatum) of having come from different areas. On the other hand, the difference between the indices calculated for flounder parasites in summer 1975 is extreme. The value of metazoan diversity from winter flounder is significantly greater, both than 1975 smooth flounder and the same index

calculated for winter flounder in 1974. I must conclude that even similar species can have drastically different parasite diversity indices. Less drastic differences were found by Davis and Huffman (1975). The change between 1974 and 1975 could not be correlated with any environmental difference, the only possible explanation might lie in the longer 1975 sampling period. It appears that if parasite diversity indices are to be utilized to compare two or more habitats, care must be exercised in selecting a representative host. More work is necessary prior to any final conclusions.

PART VII

General Conclusion

The Field investigation of parasite populations as practiced in this study, has definite strengths and weaknesses. The strengths of the method are that it reflects the complex interaction of parasites and their environment. It shows the seasonal flow of different parasite infrapopulations, the variations in these patterns in different years or between different groups of hosts, the habitat preferences, the frequency distributions and their implications, and the possible interspecific interactions, as they occur in nature. Also, field data permits parasite based inference concerning the ecology of the host. In this study the most striking examples of this are the suggestions of host movements tha t are provided by the C. lingua and G. stephani seasonal occurrence data.

Unfortunately, in most instances the investigation of natural processes must remain descriptive. The complexity of the natural situation limits the conclusions which might be drawn from field data. The factors which influence seasonal abundance cycles, habitat specificity, frequency distributions, etc. are well known; but most cannot be untangled without controlled laboratory experiments. The precise effects of temperature, diet, parasite life span, inter- and intraspecific interactions etc. need to be established for all the species involved.

A second weakness of field work in an open system such as the Lamprey River is that even description of events must take into account any restrictions, such as host migrations, imposed on the data. An argument could be made that seasonal abundance cycles are a reflection of the seasonal movement of differentially infected flounder. There is an indication of this in the C. lingua - G. stephani data for the Lamprey

River; and for a fish such as Liopsetta, whose migration are poorly known, the problem is more acute. In this case, research has shown that young winter flounder are quite sedentary (Pearcy, 1962), and intra-estuary differences in parasite fauna (Part III, this dissertaiton) indicate that mixing of smooth flounder stocks is not pronounced. The parasite abundance crycles are also consistent within the bay. On these bases, the seasonal abundance cycles found for most parasites in Lamprey River Liopsetta are probably representative of the local situation, but this assumption does not hold for the winter months, when the likelihood of host migration is increased.

As a result of reservations such as the above, the investigation of population dynamics in the field is devoid of hard explanations. It represents, however, a worthwhile and necessary first step toward understanding, and a source of intriguing questions.

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Figure 1. The Great Bay estuary, New Hampshire (LR = Lamprey River, GSB = General Sullivan Bridge, AP = Adams Point, FP = Fabyan Point).

FIGURE 1

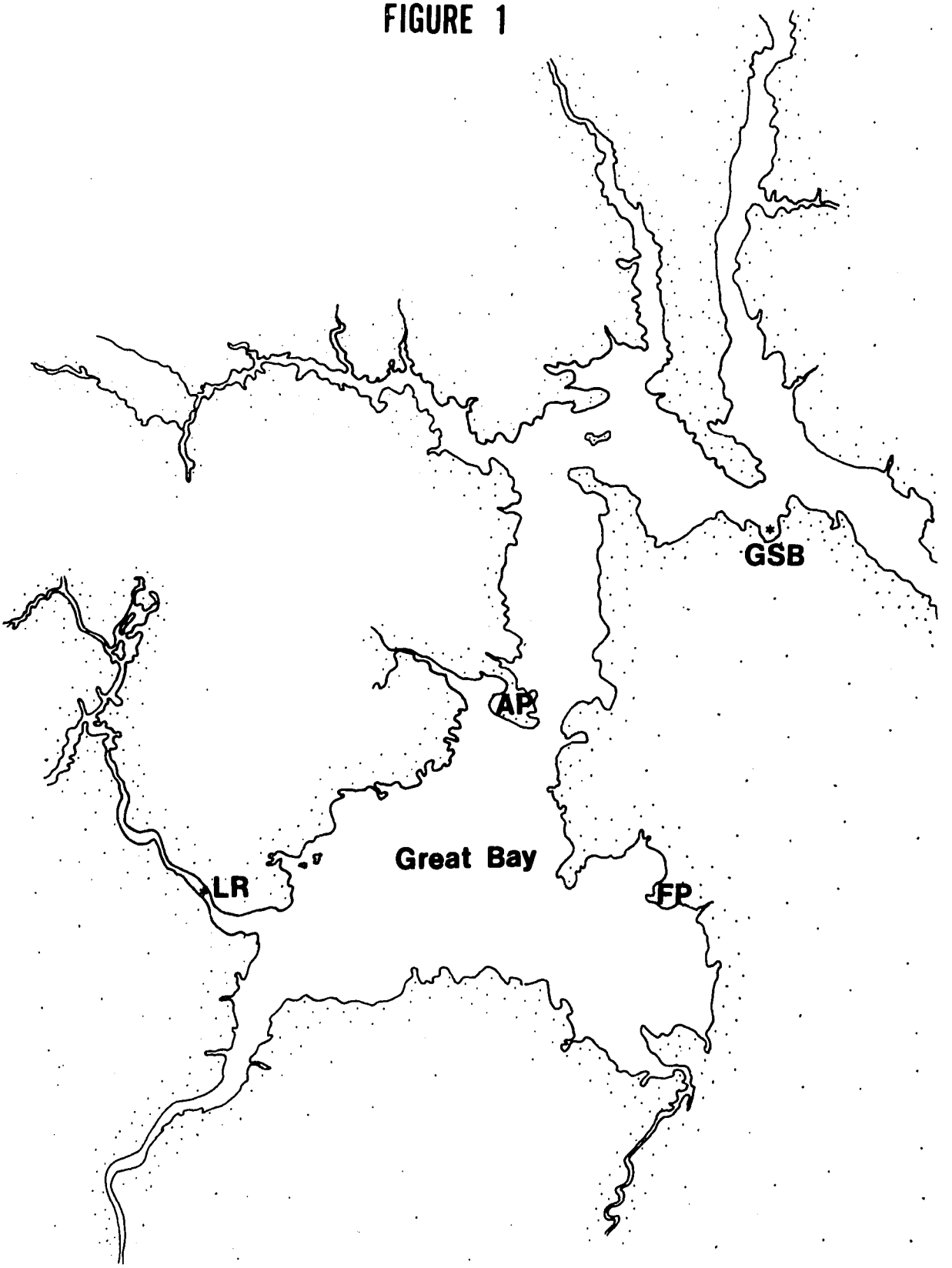

Figure 2. Unknown Sporozoan #1.

FIGURE 2

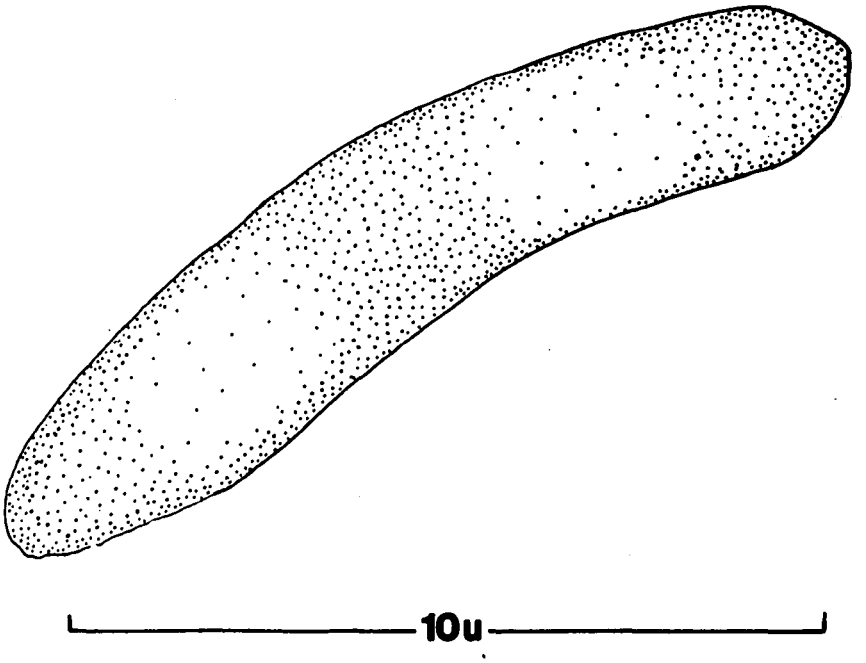

Figure 3. Unknown Sporozoan #2 in the intestine of Liopsetta putnami (100x).

Figure 4. The Lamprey River collecting site, Newmarket, N.H.

Figure 5. The General Sullivan Bridge collecting site, Newmarket, N.H.

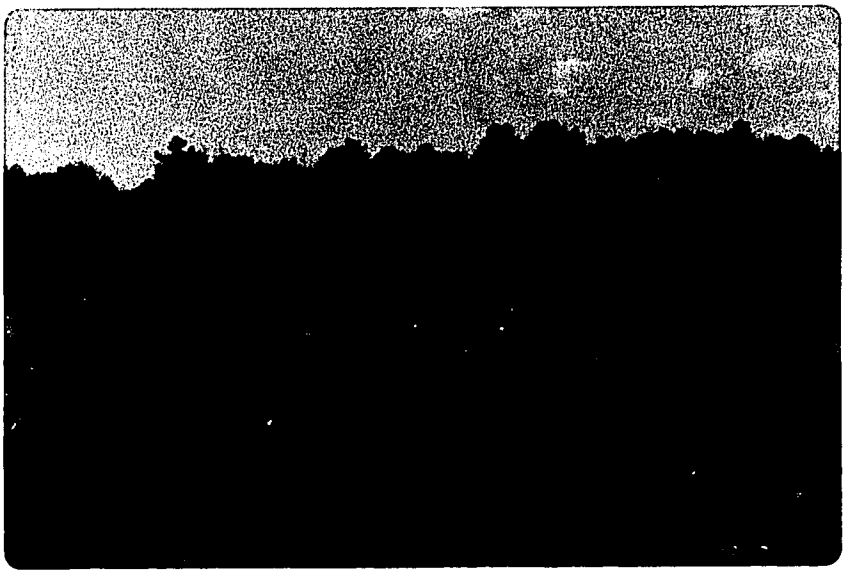

Figure 6. Surface water temperature at the Lamprey River (1975-1976).

FIGURE 6

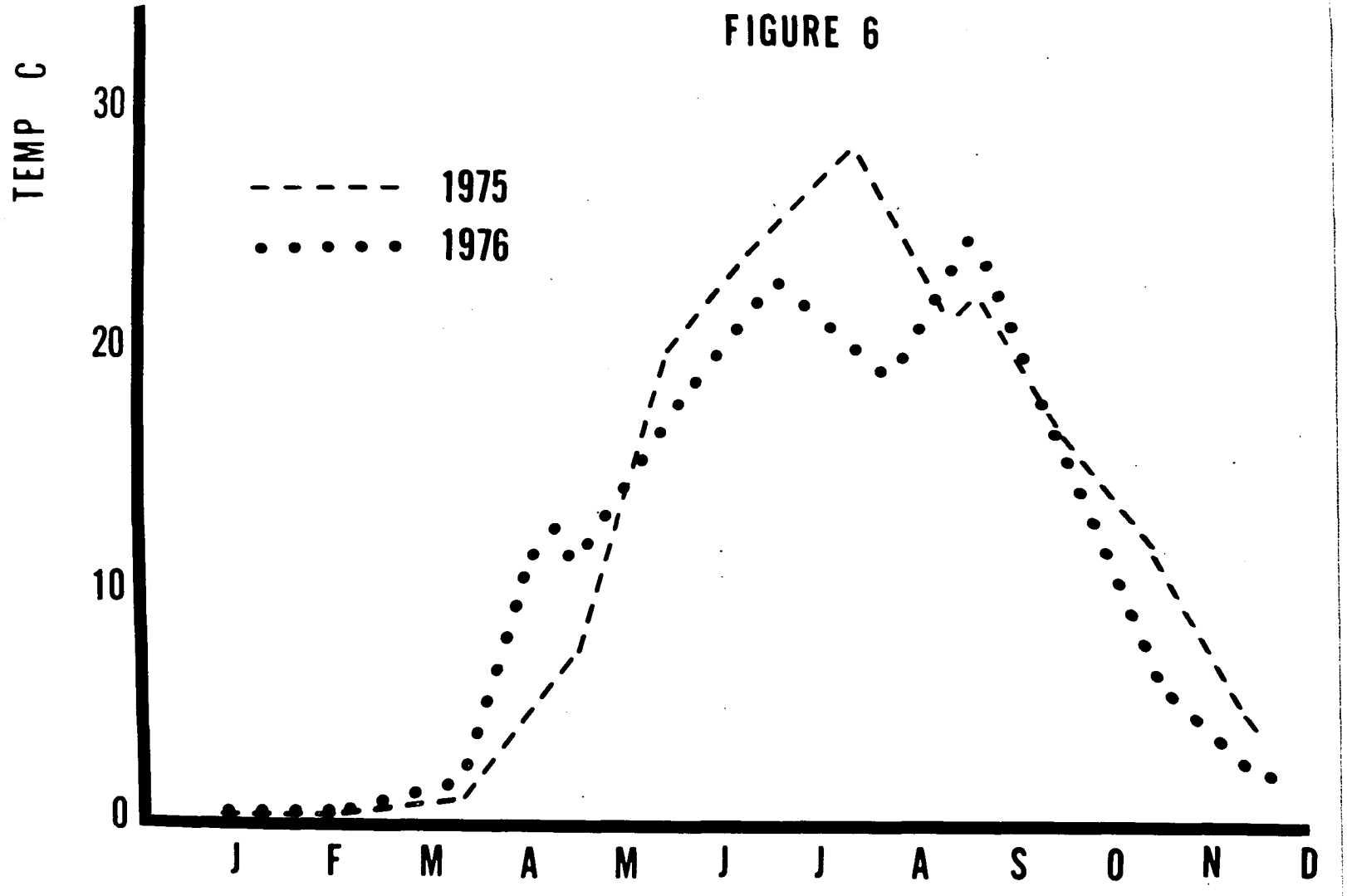

Figure 7. Salinity at the Lamprey River (1975-1976).

FIGURE 7

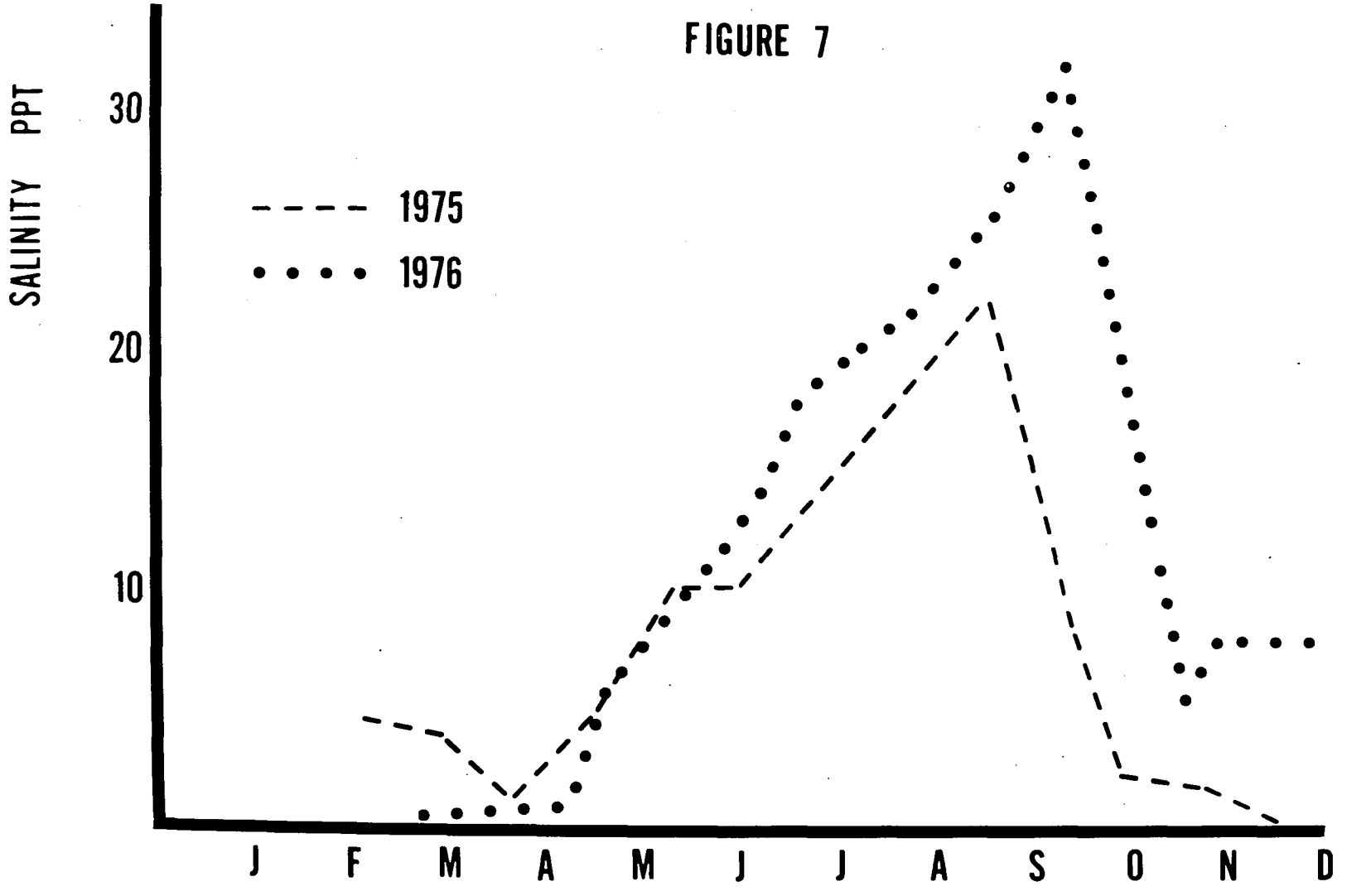

Figure 8. Relative Percentages of total infection in different gut sections of 0+ age-group smooth flounder (1975-1976) for different helminths (A - Lepocreadium setiferoides, B - Homalometron pallidum, C - Zoogonus lasius, D - Opecoeloides vitellosus, E - Lecithaster confusus, F - spirurid larva, ST - stomach, I - anterior intestine, II - mid intestine, III - posterior intestine, R - rectum). See Table 4 for data.

FIGURE 8

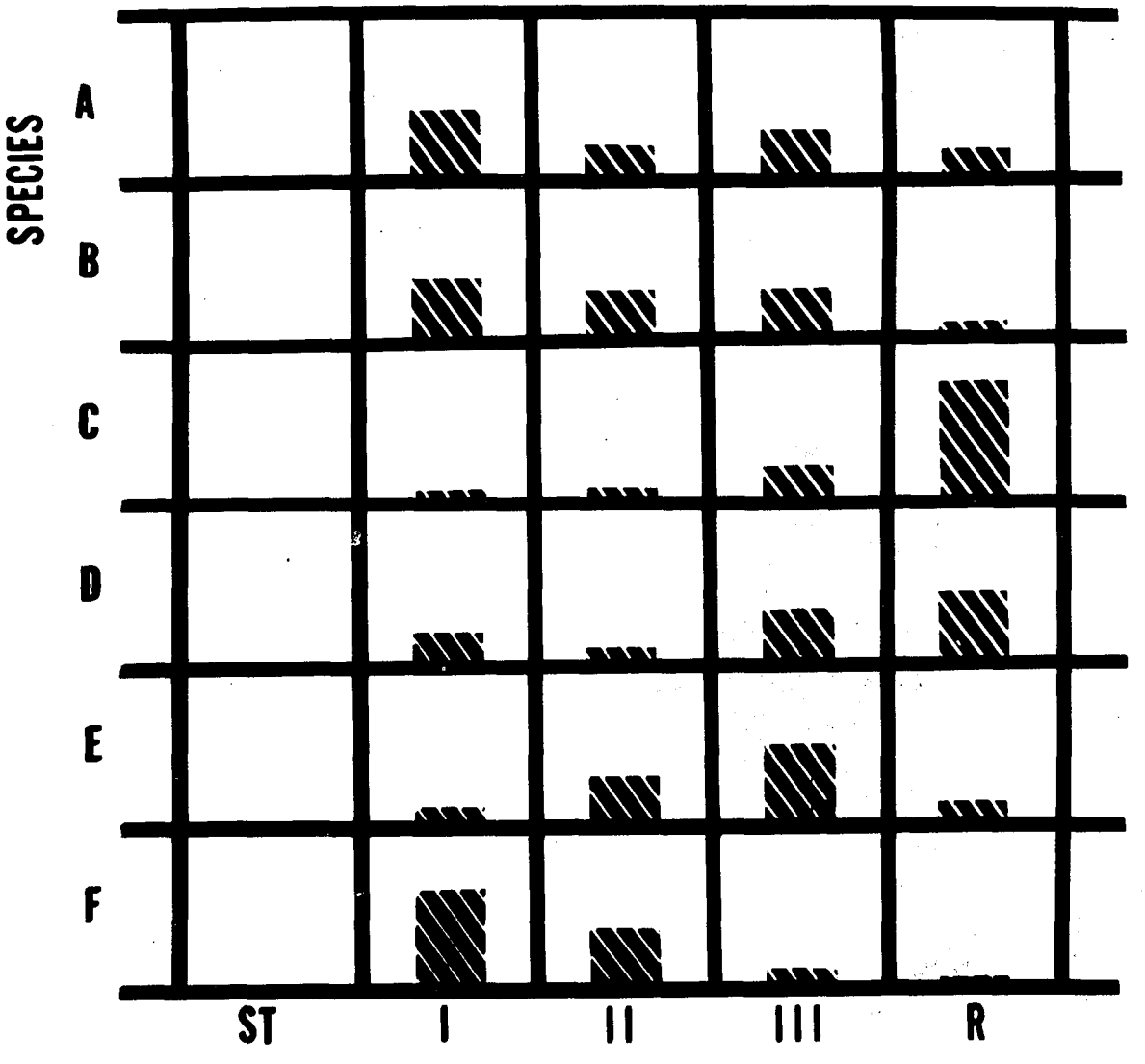

Figure 9. Relative percentages of Lepocreadium setiferoides infection in the gut sections at different population densities ($\bar{x}$ - mean no. Lepocreadium per fish, I - anterior intestine, II - mid intestine, III - posterior intestine, R - rectum). See Table 6 for data.

FIGURE 9

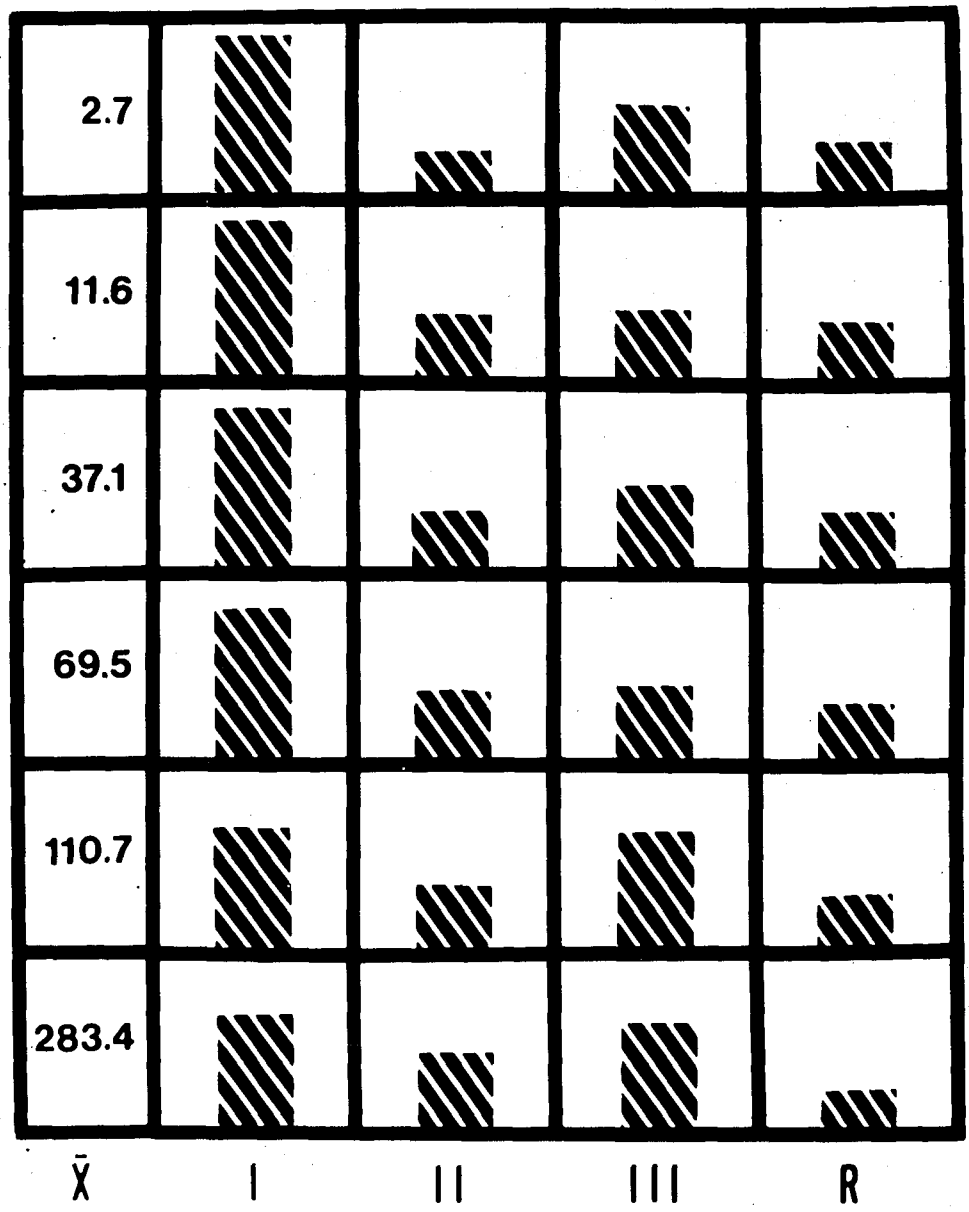

Figure 10. Relative percentages of Homalometron pallidum infection in the gut sections at different population densities ($\bar{x}$ - mean no. Homalometron per fish, I - anterior intestine, II - mid-intestine, III - posterior intestine, R - rectum). See Table 8 for data.

FIGURE 10

Figure 11. Frequency histograms for Zoogonus lasius in 0+ age-group smooth flounder in the Lamprey River (1975 and 1976).

FIGURE 11

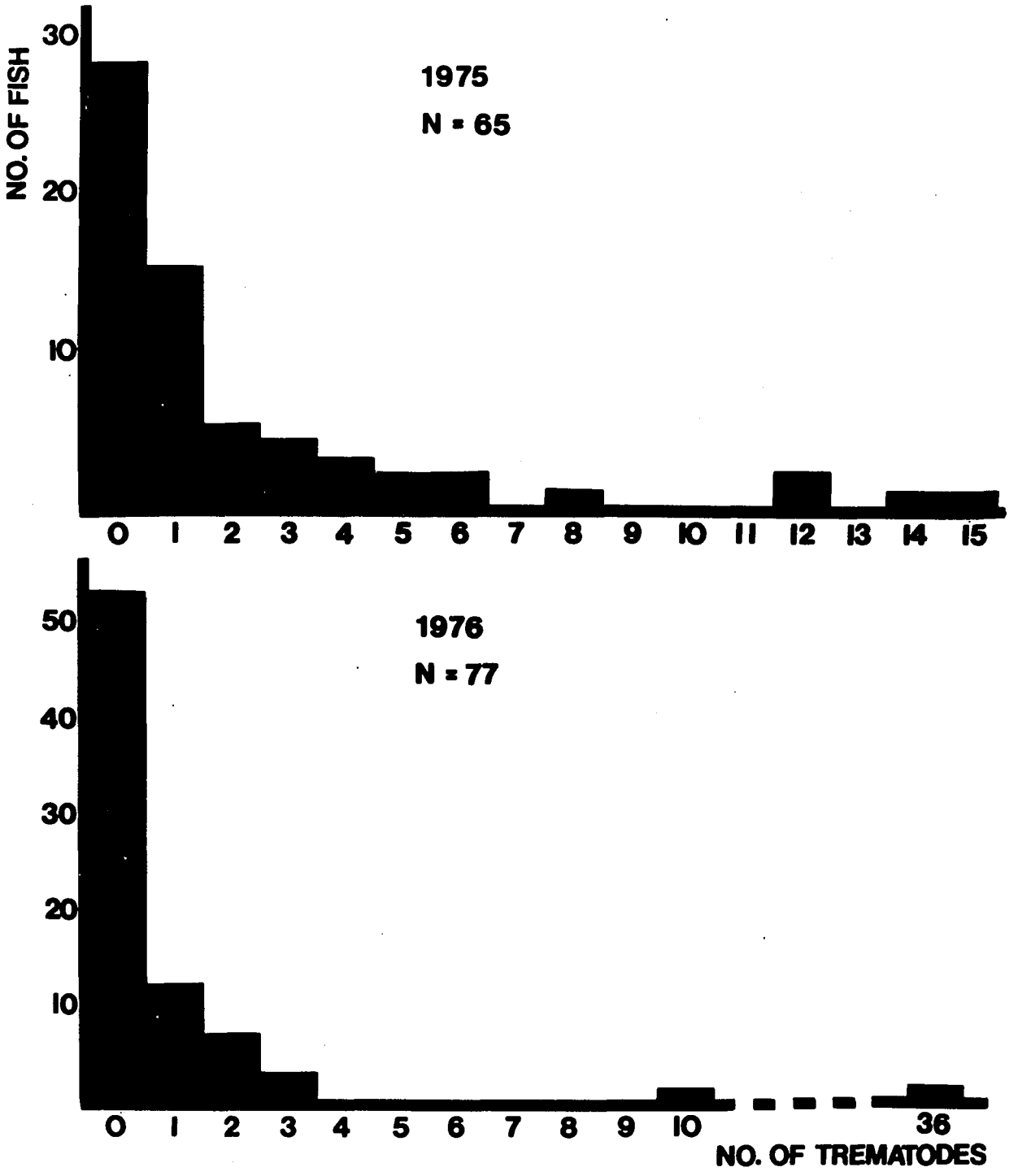
NO. OF FISH
30
20
10
1975
N = 65
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
50
40
30
20
10
1976
N = 77
0 1 2 3 4 5 6 7 8 9 10
36
NO. OF TREMATODES

Figure 12. Frequency histogram for Stephanostomum tenue in 0+ age-group smooth flounder in the Lamprey River in 1975.

FIGURE 12

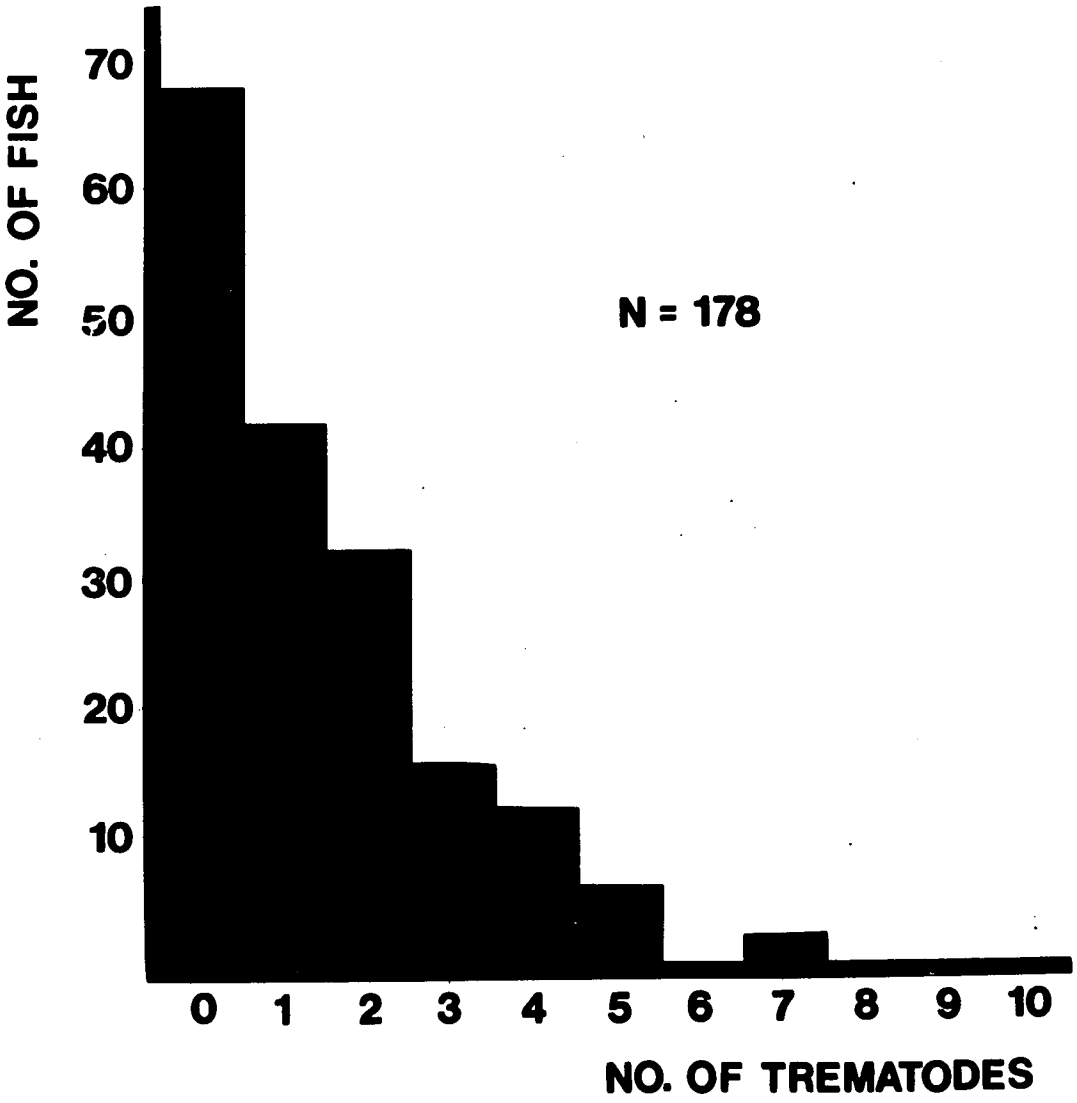
NO. OF FISH
70
60
50
40
30
20
10
N = 178
0 1 2 3 4 5 6 7 8 9 10
NO. OF TREMATODES

Figure 13. Schematic gill arch, showing dorsal, medial and ventral sections.

FIGURE 13