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POPULATION PATTERNS AND HABITAT SPECIFICITY OF *POMPHORHYNCHU BULBOCOLLI* (ACANTHOCEPHALA) IN THE INTESTINES OF WHITESUCKERS *CATOSTOMUS COMMERSONI*, FROM TYRRELL LAKE, ALBERTA, CANADA.

by

SAMUEL DZIFA AMEDJO

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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OF MASTER OF SCIENCE

ZOOLOGY

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Supervisor

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.......R. H. Gooding.......................

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Date..4 October 1988....

ABSTRACT

This study was prompted by several unsuccessful attempts at establishing laboratory infections of *Pomphorhynchus bulbocolli* in its intermediate host, *Hyallela azteca*, for laboratory experiments on rainbow trout, *Salmo gairdneri*, one of its definitive hosts. The aim of this study was, therefore, to determine whether or not all gravid female *P. bulbocolli* carry infective eggs and, also, whether or not their egg production and development are influenced by season, the site occupied in the intestine of the definitive host, and crowding.

Monthly samples of the intermediate and the definitive hosts were collected with hand and gill nets, respectively, from May through July, 1985, and from May through September, 1986, from Tyrrell Lake, a natural, saline, eutrophic lake situated approximately 52 km south-east of Lethbridge, Alberta, Canada (49° 23' N, 112° 15' W). The intestines of the definitive hosts, from oesophagus to anus, were removed and divided into 10 equal sections. The numbers of non-gravid females (without shelled eggs), and male, gravid (with shelled eggs) and ripe (with shelled acanthors) females of each of four colour morphs were determined. For each section, a sample of gravid and ripe females of each colour morph was removed, measured, and used for infection experiments.

With the exception of two, small age 1+ fish, all fishes were found infected with *Pomphorhynchus bulbocolli* in all months sampled. The statistical distribution of the numbers of worms in individual fish was markedly skewed, suggesting an aggregated distribution. Intensity of infection was found to be dependent on the sex and age of fish, being higher in females and older fish; no indication of age resistance was found. Intensity of infection was high in May through July, and decreased through August and September. Invasion by new worms occurred throughout the year and was high in spring and fall and a low in early summer (July).

Growth and development were strongly correlated with the colour of the worm. Cream-coloured worms were small, with the mean length of light yellow, yellow, and dark yellow worms increasing with intensity of colour. Eggs were relatively undeveloped in cream-coloured worms, showed increasing development in light yellow and yellow worms, and

fully developed, presumably ripe infective shelled acanthors were found only in dark yellow females. Only eggs from dark yellow females gave successful infections in *Hyallela azteca* in the laboratory, so dark yellow females were considered as ripe females (bearing shelled acanthors).

Both egg production (by gravid females) and egg release (by ripe females) depended on season, both being low in June, reaching a high in July, and decreasing the rest of the summer; in fact egg release was restricted to early summer (July).

Pomphorhynchus bulbocolli exhibited habitat specificity, about 83% of all age and sex categories of worms preferentially occupying the 60-80% region (sections 7 and 8) of the intestine. There was no evidence of any migration from one area of settlement to an area of maturation. However, small, recently acquired worms and non-gravid females were relatively more abundant in the unpreferred, less populated sites (sections 3-6, and 10), whilst gravid females were relatively more abundant in the preferred, heavily populated sites (sections 7 and 8); relatively more large, unfertilised females, those which would be expected to be fertilised but were not, occurred mainly in the 80-100% region. It is concluded that the distances separating male and female worms may have prevented copulation.

Further evidence indicated that the 80-100% region is not a suitable habitat. The older and more mature yellow and dark yellow worms were completely absent from the 80-100% region, being restricted mainly to the 60-80% region; this suggests that survival is better in the 60-80% region and poor in the 80-100% region. The cream:light yellow ratio, which should be inversely related to development, was significantly higher in the 80-100% region, suggesting that worms do not live to egg-releasing age in this region. And generally, male and gravid females in section 10 were significantly smaller in size than those in other sections.

Evidence is provided to suggest that in the search for a densify-dependent process capable of regulating the size of intestinal helminth populations in the definitive host, the feeding habits of the host should be taken into consideration, not only its age or size. Evidence obtained on the effect of crowding on the population of *Pomphorhynchus bulbocolli* was not conclusive.

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When I arrived in Canada to begin my studies, little did I know that my programme was going to take five years. It was a long and winding path full of problems, obstacles, and frustrations but through the encouragement, help, and support from my supervisor, the Department, and a number of people, it has finally come to a successful end.

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I. INTRODUCTION

The use of permanent saline lakes for sport fisheries is of considerable interest in the western prairies of Canada. One such lake is Tyrrell Lake, southeast of Lethbridge, Alberta, which has been stocked with rainbow trout, *Salmo gairdneri*, and managed as a sport fishery since 1962.

Tyrrell Lake is a natural lake located within a shallow basin, surrounded by highly mineralised soils in an arid region with strong winds, warm summer temperatures and fluctuating water levels. It is a closed system with no outflow into the drainage system, except when water levels are exceptionally high (Fitch, 1980). Lower lake levels, therefore, result in high salinity, predominantly sulphate, bicarbonate and sodium. The lake is eutrophic, with a high biological productivity (Fitch, 1980).

Planting of rainbow trout began in 1962; this was followed by further stockings in 1963, 1966, 1970 and 1971, and annually from 1974 through 1985. The growth rate of the introduced rainbow trout was found to be two to three and half times faster than trout of the same origin stocked in other southern Alberta lakes; daily growth rates were as high or higher than reported in the literature for the species. The stocking density had no effect on the growth rate (Fitch, 1980).

The exceptionally high growth rate, however, was accompanied by limited survival. Prior to 1974, the catch consisted of age classes 0+, 1+, 2+ and 3+ (79, 19, 2 and 0.2% respectively) but since 1974 it consisted almost exclusively of 0+ and 1+ (92 and 8%, respectively). By 1980, survival rates were 13% for age class 0+ to 1+, 3.8% for 1+ to 2+, and zero for older age classes. Tyrrell Lake, therefore, presents a fisheries management problem in that even though growth rates are high, survival is very poor. This poor survival has been ascribed to a number of factors, including high salinity, high summer temperatures, low summer oxygen levels (Fitch, 1980) and parasites.

High salinity, in itself, does not seem to be a problem. Rainbow trout survive TDS concentrations of up to 19,340 mg/l and sulphates up to 9600 mg/l in a highly saline Wyoming lake (Gordon, 1963). Gordon (1963) also indicated that rainbow trout are euryhaline and survive well in both freshwater and the sea. They have been successful in aquaculture operations in brackish water (Murai and Andrews, 1972; Tatum, 1973) and in seawater (Brett, 1974). Thus, rainbow trout are known to tolerate a wide range of water chemistry conditions and can survive well under conditions more extreme than those of Tyrrell Lake (Fitch, 1980).

Fitch (1980) suggested that severe temperatures could be caused by a combination of high ambient temperature, low wind action and low lake levels, conditions which do occur at the lake. The literature contains conflicting reports on the effect of temperature on rainbow trout. Cherry, Dickson and Cairns (1977) reported a lethal temperature of 27°C, whilst Soldwedel and Pyle (1968) observed survival at 29°C. Such high temperatures have been recorded only once at Tyrrell Lake. It is possible that the duration of the lethal temperature may be an important factor; if so, temperature is probably not a limiting factor, because of the fairly uniform summer temperatures (Fitch, 1980).

Davis (1975) reported that oxygen levels below 6 mg/l caused respiratory problems in rainbow trout and that the minimal requirement is affected by acclimation, temperature, water chemistry and fish size. Dissolved oxygen is at its lowest in mid-summer in Tyrrell Lake. A critical level of less than 3 mg/l was found in July, 1977, but there was no evidence of a fish kill associated with this condition, and survival rates were higher than in previous years (Fitch, 1980). In addition, Fitch (1980) reported winter oxygen levels less than 6 mg/l in, at least, four out of ten years. Between October, 1978, and May, 1979, there was a significant reduction in the trout population, at a time when oxygen levels were usually 5 mg/l or more. Fitch (1980) recognised the potential of oxygen as a limiting factor but concluded that the poor overwinter survival was not due solely to oxygen levels. Rao (1968, 1971) investigated the influence of salinity on oxygen consumption in rainbow trout and found that oxygen consumption was lowest at 7500 mg/l and that the consumption at 7500 mg/l was not significantly differen from that at 15,000 mg/l. Since salinities at Tyrrell Lake exceed 7500 mg/l, the interaction of salinity and oxygen levels is probably not an important factor.

Reduced overwinter survival was observed starting in the winter of 1978; at about the same time, large numbers of intestinal worms were noted in the fish. It was realised that the presence of parasites could be an important factor in fish survival. Therefore, a sample of 12 rainbow trout was sent to Dr. J. C. Holmes, University of Alberta, Canada, for examination of parasites in January, 1982. All twelve fishes had extensive numbers of the acanthocephalan *Pomphorhynchus bulbocolli* in their intestines, concentrated mainly in the mid- and hind-gut where ion regulation occurs (Ando *et al.*, 1975). No other parasites were found. Like other species of *Pomphorhynchus*, *P. bulbocolli* penetrate deeply into the intestinal wall, to or even through the serosa, disrupting the muscularis and stimulating an extensive tissue capsule, and also erode the mucosal surfaces they contact (Chaircharn and Bullock, 1967; Hine and Kennedy, 1974a; McDonough and Gleason, 1981). In heavy infections, they stimulate extensive adhesions that bind together loops of the intestine or even bind the intestine to other organs or to the body wall (Dr. J. C. Holmes, personal communication). One obvious conclusion was that the parasite could have a very considerable influence on the digestive physiology and ion regulation mechanisms of rainbow trout.

There is abundant evidence in the literature that parasites do have a negative impact on their hosts and may kill them. However, Holmes (1982) argued that the pathogenicity of helminth parasites depends largely on synergism with other agents, including predators (Holmes and Bethel, 1972; Anderson, 1979), weather patterns (Holmes, Samuel and Stelfox, unpublished), genetic background of the host (Wakelin, 1978), the degree and effectiveness of the host's immune system (Mitchell, 1979), the host's general condition or plane of nutrition (Anderson, 1979), social status (Jenkins *et al.*, 1964) or amount of stress (Ould and Welch, 1980; Anderson and May, 1981). That the impact of parasites on their hosts involves synergism with other factors is the subject of current research (Ash and Crompton, 1984). Crompton and Hall (1981) stressed the importance and complexity of these relationships.

The observed pathology, together with the high salinity of the lake, prompted a study on whether or not *P. bulbocolli* has any influence on the host's feeding, assimilation efficiency, growth, mortality and ion regulation mechanism sufficient enough to cause the observed low overwinter survival. However, the proposed study of the synergistic effects of parasite load and salinity on rainbow trout was not possible. It required a steady source of infected intermediate hosts, *Hyallela azteca*, which were not readily available in the field. Therefore, it was necessary to establish a laboratory supply of infected intermediate hosts. Several attempts at establishing the laboratory supply of larvae failed, and it became evident that more information on the basic life history of the parasite was required. Apparently, Jensen's (1952) report on the life history of the parasite lacked some vital information. These experiments failed probably because not all gravid female *Pomphorhynchus bulbocolli* carry infective eggs and, also, egg production and development are influenced by season, the site occupied in the intestine of the definitive host, and crowding.

ACANTHOCEPHALAN LIFE HISTORY PATTERNS

Reproduction

The terms mature (capable of producing ova) and gravid (egg-bearing) have been used, sometimes interchangeably, to describe the reproductive condition of female acanthocephalans. A brief description of the reproductive system, as provided by Crompton (1985), will serve to distinguish between sexually mature, gravid, and ripe female acanthocephalans.

The reproductive system of female acanthocephalans consists of three main parts: 1) gonads from which ovarian balls develop to produce oocytes and, eventually, eggs (or shelled acanthors), 2) ligament sacs, and 3) an efferent duct system made up of a uterine bell, uterus, and vagina. The ligament sacs are hollow tubes in the pseudocoel which extend from the proboscis to the uterine bell. In Archiacanthocephala and Eoacanthocephala they are paired, a dorsal and a ventral one which lie in contact with each other. Palaeacanthocephala have only one ligament sac which ruptures early in sexual development.

The reproductive system of immature female acanthocephalans consists of ovaries located within the dorsal ligament sac (in Archi- and Eoacanthocephala) or in the single ligament sac in Palaeacanthocephala. The ovaries break up into fragments, termed ovarian balls, that float freely in the pseudocoel (after rupture of the ligament sac in Palaeacanthocephala) or in the dorsal ligament sac. The ovarian balls consist of a central syncytium from which oogonia (uninucleate cells) separate, passing to the periphery where oogenesis continues, eventually producing mature oocytes (the fertilisable unit) which lie just beneath the surface of the ovarian ball. At this stage, the female is sexually mature and capable of being fertilised. (The term "mature" should be used for females which have reached this stage, but it is frequently used to refer to any female containing only ovarian balls.) During copulation the male grasps and surrounds the posterior end of the female with its everted bursa, and sperm are discharged into the uterus via the vagina. The male then discharges a cement secretion which sets as a plug, the cement plug, in the gonopore of the female, preventing the escape of spermatozoa. The spermatozoa pass from the vagina, up the uterus to the uterine bell from which they escape into the pseudocoelom amongst the ovarian balls. The spermatozoa penetrate the surface of the ovarian balls and enter the mature oocytes, their cytoplasms and nuclei fusing to form the zygote. A fertilisation membrane is produced to block polyspermy; this membrane becomes the outer envelope of the egg or shelled acanthor. Cleavage begins while the zygote is still attached to the ovarian ball, but the embryo soon detaches from the ovarian ball and floats free in the pseudocoelom, where further development occurs. As it develops, some of the nuclei continue to divide, with some of the resulting cells developing into a series of membranes, so that the mature embryo or shelled acanthor has three or four membranes, depending on species. Most of the nuclei, however, contract into tiny, dense bodies which begin migrating inward to form a central nuclear mass (or mesoderm) which will develop into all the adult structures, except the tegument and lemnisci. Further development of the mature, shelled acanthor cannot occur until they are eaten by the proper intermediate host.

Normally, the membranes and the central nuclear mass develop at the same time, so that fully shelled acanthors have a fully developed central nuclear mass. Females with these shelled acanthors, with nuclei well concentrated in the centre or fully developed central nuclear mass, and surrounded by the full complement of membranes, are called gravid females. However, in some acanthocephalans, such as *Pomphorhynchus bulbocolli*, the egg membranes (shells) develop more rapidly (or under different conditions) than the embryo itself; in such cases, females with shelled eggs are "gravid" females, whereas those with a fully developed central nuclear mass are "ripe".

There are two main ways in which the mature, shelled acanthors can get to the intermediate host. In some species of acanthocephalans, the entire female body is shed as a bag of eggs or shelled acanthors by the definitive host into the environment, and the shelled acanthors are released on disintegration of the body. In other species, the shelled acanthors are moved from the pseudocoelom into the dorsal ligament sac from where they are engulfed into the uterine bell. The uterine bell sorts out the shelled acanthors, returning immature ones to the pseudocoelom; mature ones are passed through the uterus into the vagina and, eventually, end up with the intestinal contents of the definitive host and passed out with the faeces.

In some acanthocephalans, such as *Echinorhynchus truttae*, cystacanths (the infective juvenile in the intermediate host) become sexually mature in the intermediate host and copulation starts about three days after establishment in the definitive host (Awachie, 1966); therefore, all females in the definitive host are sexually mature and can become fertilised (and gravid) shortly after establishment in the definitive host. Other species of acanthocephalans, for example *Pomphorhynchus bulbocolli*, must undergo a period of several weeks of growth and development in the the definitive host before becoming sexually mature (Jensen, 1952); only then are the females capable of becoming fertilised and gravid.

Seasonal Patterns

Of the factors that are known to influence acanthocephalan life history patterns, seasonal patterns have attracted the most attention. The seasonal patterns of prevalence and intensity of infection, recruitment, loss, sexual maturation, egg production, and egg release in parasitic helminths (including acanthocephalans) in freshwater fishes, and the factors, abiotic and biotic, which influence them, have been extensively reviewed by Chubb (1982). Chubb (1982) also took a look at the seasonal patterns of occurrence of parasitic helminths in five major climatic zones, including the subpolar region where Alberta, Canada, (and the present study) is located. He showed that, even within a climatic zone, there are considerable differences in the seasonal patterns of occurrence for some species and, furthermore, warned that care must be taken in making inter-zone comparisons.

Some, but not all, species of parasitic helminths in the subpolar climatic zone show a clear seasonal pattern of prevalence and intensity of infection, and recruitment in the definitive host, and this may or may not vary from one geographical location to the next. For example, in the U.S.S.R., maximal prevalence and intensity of infection with *Neoechinorhynchus rutili* occurred during winter and spring in *Lota lota*, but in spring and summer in *Rutilus rutilus*; recruitment occurred all year round (Malakhova, 1961). Leong (1975) reported that in Cold Lake, Alberta, *Echinorhynchus salmonis* showed peaks of prevalence and intensity of infection in *Coregonus clupeaformis* in both midsummer (July) and early winter (December), but showed no seasonal pattern in *Coregonus artedii*; recruitment into both hosts was more or less constant throughout the year. In *Coregonus nasus* collected from the Bay of Bothnia, Finland, prevalence of *E. salmonis* was low in winter, increased to a peak in midsummer, and decreased through the rest of the summer and fall, whereas the intensity of infection showed no clear patterns; recruitment occurred in early summer, autumn, and winter (Valtonen, 1979). It is clear from these examples that parasitic helminths do not necessarily show the same pattern wherever they occur.

A number of factors are known to be involved in the production of seasonal patterns of prevalence and intensity of infection, recruitment, and loss. These factors include availability of infective larvae and the feeding pattern of the definitive host, extreme temperature variations, and the immune response of the host.

Awachie (1965) found that the intensity of infection of *Echinorhynchus truttae* in brown trout was high in summer (June through September) and low in fall and winter (October through April); he correlated this pattern with the seasonal variation in the feeding activity of the trout, as determined by changes in temperature.

Interaction of temperature and host immune response also tends [illegible]nce seasonal cycles of occurrence of parasitic helminths. Avtalion *et al.* (1973), Corbel (1975), and Cottrell (1977) have shown that the fish immune system depends on temperature and is more evident and rapid in action above 10°C. Kennedy and Walker (1969) hypothesised that seasonal changes in resistance to infections were directly dependent on temperature. They found that in winter when temperatures were low, resistance was also low, facilitating establishment of *Caryophyllaeus laticeps* in dace; rising temperatures in spring increased resistance to new invasions. Higher summer temperatures increased resistance to a point where not only newly acquired worms were eliminated but also already established ones were lost. They concluded, on the basis of laboratory experiments, that a strong temperature-dependent response by the fish was responsible for the disappearance of *C. laticeps* in summer. On the other hand, *Pomphorhynchus laevis*, which does not exhibit a seasonal cycle, showed a much weaker response to the host immune system at higher temperatures (Kennedy, 1971). This hypothesis has been applied to explain summer loss by Kennedy and Walker (1969), Awachie (1972), Anderson (1974, 1976), Eure (1976), Moravec (1979) and others. However, Kennedy and Walker (1969) could not detect any antibodies to the antigens of *Caryophyllaeus laticeps* in *Leuciscus leuciscus*. Furthermore, Harris (1972) has demonstrated that *Leuciscus cephalus* produced precipitins against *Pomphorhynchus laevis*, but worm numbers were not affected. Harris (1972) suggested that the immune system is not important, at least in some species, and McArthur (1978) contends that the role of the fish immune system against helminth parasites is uncertain. Natural mortality of already established worms may also account for the seasonal loss of adults as observed by Kennedy (1972c) where host reaction to *P. laevis* was unable to eliminate the worms, even though the worms provoked antibody production.

Chubb (1982) recognised four broad groups of parasitic helminths based on the time of year when they invade and become established in the definitive host. These are invasion 1) in early spring through early summer, for example *Neoechinorhynchus rutili* in *Cyprinus carpio* from Czechoslovakia (Tesarcik, 1970, 1972), and *Pomphorhynchus bosniacus* in

Leuciscus cephalus albus from Yugoslavia (Kazic, 1970); 2) in summer through autumn or early winter, for example *Neoechinorhynchus tumidus* in coregonids from U.S.S.R. (Bauer, 1959a); 3) in autumn, winter and early spring, for example *Echinorhynchus salmonis* in *Perca flavescens* from Lake Ontario, Canada (Tedla and Fernando, 1969, 1970), and *Acanthocephalus parksidei* in *Catostomus commersoni, Lepomis cyanellus, Semotilus atromaculatus*, and eight other fishes from Pike River, Wisconsin (Amin, 1975b); and 4) all year round, even though establishment may be higher at one period of the year, for example *Echinorhynchus truttae* in *Salmo trutta* from a stream in Wales (Awachie, 1965) and *Pomphorhynchus laevis* in *Leuciscus leuciscus* (Hine, 1970), *L. cephalus* (Kennedy, 1972c), and *Cottus gobio* (Rumpus, 1975), all from River Avon, England. The first three groups exhibit a strong seasonal pattern, the fourth a limited one.

It is evident from the literature that in some species, loss of parasites is tied to egg release. Muzzall and Rabalais (1975a, b), for example, reported that in July the population of adult *Acanthocephalus jacksoni* declined abruptly so that by the end of summer none was present in the intestines of the hosts. The female worms, containing shelled acanthors, were passed out whole and, in some fishes, could be seen hanging out of the anus. They suggested that the shelled acanthors were released through disintegration of the female worms after they have been voided. A similar situation has been reported for *Acanthocephalus lucii* in *Perca fluviatilis* by Komarova (1950). Komarova (1950) indicated that in summer adult parasites di and shelled acanthors are released by gravid females.

Chubb (1982) recognised four main seasonal patterns of egg production (and release?): 1) gravid from spring to early summer, e.g., *Proteocephalus percae* in *Perca fluviatilis* from U.S.S.R. (Ieshko *et al.*, 1976), and *Triaenophorus nodulus* in *Esox lucius* from Wales (Chubb, 1963) and U.S.S.R (Kuperman, 1973); 2) gravid late spring to summer, e.g., *Neoechinorhynchus tumidus* in coregonids from U.S.S.R. (Bauer, 1959a); 3) gravid spring to autumn, e.g., *Leptorhynchoides thecatus* in *Ambloplites rupestris* from Wisconsin (De Giusti, 1949) and *Neoechinorhynchus longirostris* in *Dorosoma cepedianum* from Illinois (Jilek, 1978) and 4) some gravid individuals present every month in mid-latitude zones, even though peak egg production is probably during summer, e.g., *Acanthocephalus lucii* in *Perca fluviatilis* from U.S.S.R. (Malakhova, 1961) or *Lota lota* from U.S.S.R. (Shul'man *et al.*, 1974); *Echinorhynchus salmonis* in *Coregonus artedii* and *C. clupeaformis* from Cold Lake, Alberta (Leong, 1975; Holmes *et al.*, 1977), *Osmerus mordax* from Lake Michigan (Amin and Burrows, 1977), and *Coregonus nasus* from Finland (Valtonen, 1980a, b); and *Pomphorhynchus bulbocolli* in *Castostomus commersoni* from Maine (Lawrence, 1970), and in *C. commersoni*, *Cyprinus carpio*, and other fish species from Silver and Tichigan Lakes, Michigan (Amin, 1987a). The first three groups show a marked seasonal pattern, the fourth a limited one.

A number of factors have been suggested to influence maturation of helminth parasites in fish. The most frequently suggested factor is temperature. In his study of *Neoechinorhynchus tumidus* in coregonids, Bauer (1959b) reported that at the end of June and beginning of July the acanthocephalans were small and immature; in September large worms, the females with shelled acanthors, were found. Jilek (1978), working on *N. longirostris* in *Dorosoma cepidianum* at Crab Orchard Lake, Illinois, U.S.A. noted only immature worms in March. Sexually mature worms were found in late March, and throughout the spring and summer; he suggested that higher temperatures were responsible for the sexual maturation of the worms. This stimulatory effect of high temperature on growth and sexual maturation has been reported by several workers, including Amin (1987a) for *Pomphorhynchus bulbocolli*.

Chubb (1967) also pointed out the similarity in times of sexual maturation of different species in different hosts and the correlation with temperature and suggested temperature as the causal factor. However, Kennedy (1975) pointed out that, because of lack of experimental evidence, this suggestion should be applied with caution. The reason for caution is best illustrated by *Proteocephalus percae* in *Perca fluviatilis*.

Willemse (1965, 1969) demonstrated that when water temperature was increased in a tank containing *P. fluviatilis* infected with undifferentiated *Proteocephalus percae*, rapid differentiation of the cestodes into mature worms with normal genitalia resulted and concluded that sexual maturation was controlled by temperature. However, Wootten (1974) observed that sexual maturation of the cestode population commenced in December and January when water temperature was 2-7.5°C and was still falling. Wootten (1974) also observed that sexual maturation of the cestodes coincided with maturation and spawning of *P. fluviatilis* and concluded that endocrine levels of the host might be involved in sexual maturation of this and other cestodes. Similar close relationships between sexual maturation of helminth parasites and maturation of their hosts have been documented by several workers, including Amin (1975b) for *Acanthocephalus parksidei* and Amin (1978) for *Echinorhynchus salmonis*. However, other instances are known where host hormones, apparently, have no influence on maturation. For example, Muzzall and Bullock (1978) observed gravid worms of *Neoechinorhynchus saginatus* in both small, sexually immature and large, sexually mature *Semotilus corporalis*.

In some species, the sexual maturation and egg production pattern is associated with the availability of the intermediate hosts. Muzzall and Rabalais (1975a), for example, found gravid worms of *Acanthocephalus jacksoni* in all months except August to October, a period when the intermediate host, *Lirceus lineatus*, was absent. In *Neoechinorhynchus rutili*, Walkey (1967) found females with shelled acanthors in all months over a two-year period, but there was a marked annual sexual maturation and egg production cycle which coincided with a seasonal availability of the intermediate host, even though temperature initiated the process.

Habitat Specificity

Seasonal patterns of migration along the length of the alimentary tract of fishes to favourable sites have been reported (Amin, 1975b; Amin and Burrows, 1977; Tedla and Fernando, 1969, 1970; Valtonen, 1980b; and others). In some species of parasitic helminths, there are even seasonal differences in distribution along the length of the alimentary tract, e.g. *Neoechinorhynchus cylindratus* and *N. proxiloides* (Amin, 1986). The distribution and survival of parasitic helminths in the alimentary tract has been assumed to be dependent on the phases of digestive activity or inactivity, and the morphology, histology, or physiology of the alimentary tract (Crompton, 1973). Study of the distribution of helminth parasites and the sites they occupy would, therefore, lead to a better understanding of the factors that affect their population density, establishment, survival, nutrition, growth, maturation, and reproduction (Crompton, 1973). The question, then, which immediately comes to mind is whether or not there is a relationship between the site occupied and how well the parasite does.

Crompton (1973) has reviewed the events that lead to the establishment of adult helminths in their sites and recognises three main groups. Group 1 are those whose immature stages arrive directly at the site of adults, e.g. *Polymorphus minutus* (Crompton and Whitfield, 1968; Lingard and Crompton, 1972) and *Pomphorhynchus laevis* (Kennedy *et al.*, 1976). In all these cases, no difference was found in attachment sites between male and female worms and there was no movement up or down the alimentary tract. Kennedy *et al.* (1976) reported that *P. laevis* prefers a particular region of the intestine but can establish, survive, and grow in other regions as well. The greatest mean and maximum lengths were recorded in the preferred region, both measures declining anteriorly and posteriorly. Kennedy *et al.* (1976) concluded that only unsuitable physico-chemical or feeding conditions affect the growth of the parasite, not the site it occupies. However, the differences in size (egg production?) between the preferred and unpreferred sites may be an indication of differences in fitness. Hutchinson (1959), working on *Hydatigera taeniaeformis*, gave an indication that fitness may depend on the site occupied since worms located in the posterior, unpreferred region had abnormally low glycogen content and were below average size. On the other hand, differences in size could be due to differences in age, which cannot be determined for worms in natural infections. Differences in age should be reflected in differences in the distribution of immature and mature worms. No such differences were found (Kennedy *et al*, 1976), suggesting that the differences observed were due to differences in fitness between sites.

Group 2 is comprised of species in which there is emigration of immature stages in the direction of gastrointestinal flow to the site of adults, e.g., *Acanthocephalus jacksoni* (Bullock, 1963), *Echinorhynchus truttae* (Awachie, 1966), and *E. salmonis* (Valtonen, 1980b). Valtonen (1980b) studied the sex ratio, body length, and embryonic development of *E.*

salmonis in relation to season and site occupied in whitefish and found that most of the parasites were situated in the posteriormost third (part C) of the intestine in all seasons. The male:female ratio in sites A, B, and C were 1.8:1, 1:2.7, and 1:6.9 respectively. Males in the three sections were essentially the same size, but females in sections A and B were significantly shorter than those in C, and their ovaries were mostly at the ovarian ball stage, whilst most of the females in section C had shelled acanthors. Valtonen (1980b) concluded that the first and second portions are equally important because the parasites can grow and mature there but do not stay there for long. The differences in fitness observed are confounded with age and the importance of the site occupied cannot be determined independently.

To the third group belong species like *Moniliformis dubius* (Burlingame and Chandler, 1941), whose immature stages emigrate against the direction of gastrointestinal flow to the site of the adults. During the course of infection of *M. dubius* in rats, the position of the worms moved steadily forward (Burlingame and Chandler, 19[illegible]. Most of the worms became attached in a zone beginning 10 cm behind the stomach and extending to 60 cm behind the stomach. Burlingame and Chandler (1941) regarded this area of the intestine as the zone of viability for *M. dubius* because worms which failed to establish themselves in this zone or failed to move into it early in their development did not survive. Maximum growth occurred in the anterior part of this zone, in spite of more crowding.

It appears that habitat specificity, at least in some species in groups 2 and 3, is correlated with biochemical changes in the developing worm (Goodchild and Wells, 1957; Archer and Hopkins, 1958; Hopkins and Hutchinson, 1958; Mettrick and Cannon, 1970; Uglem and Beck, 1972). In the most revealing study, Uglem and Beck (1972) have demonstrated that in concurrent infections of *Neoechinorhynchus cristatus* and *Neoechinorhynchus crassus* in large-scale sucker, *Catostomus macrocheilus*, *N. crassus* attached in the anterior intestine, whilst *N. cristatus* occupied the posterior intestine. Subadults of *N. cristatus* had a mean attachment point 6 cm anterior to that of adults and occupied a length of intestine twice that occupied by adults. No difference was found in the distribution of adult and subadult *N. crassus*. They demonstrated that young *N. cristatus* possessed more APase (aminopeptidase) activity per milligram of worm protein than did adults. As the worms grew and developed there was a loss of APase activity, a posterior migration of the population, and an increase in habitat specificity. *N. crassus* (group 1, according to Crompton, 1973), on the other hand, neither migrated nor showed appreciable changes in APase activity with age, suggesting that the decreased APase activity with age in *N. cristatus* is correlated with its posterior migration and increased habitat specificity (Uglem and Beck, 1972). Uglem and Beck (1972) further observed a relationship between worm APase activity and worm location in the intestine. They demonstrated that the anterior host intestine, which was occupied by *N. crassus* (with less APase activity), had a high APase activity, whilst *N. cristatus* (which had a high APase activity) occupied the posterior intestine which was nearly devoid of APase activity. Thus, if a parasite was located where APase activity in host intestinal tissue was high, it was less dependent on its own APase activity. In other words, the location of the parasite is correlated with its APase requirements. In groups 2 and 3, therefore, the site may be actively selected in response to changes in physiology associated with ageing.

Crowding

The preferential occupation of specific regions of the intestine may lead to crowding, the level of which may be related to the age or size of the definitive host. Brown (1986) demonstrated in laboratory infections that within each size class of rainbow trout, there was a ceiling level of intensity of infection with *Pomphorhynchus laevis* and correlated this level with the size of available gut habitat. He suggested that this was a density-dependent process capable of regulating parasite population size. This hypothesis has also been demonstrated by Uznanski and Nickol (1982) in a laboratory population of *Lepomis cyanellus* infected with *Leptorhynchoides thecatus*.

Brown (1986) applied this idea to a natural infection of *Pomphorhynchus laevis* in *Leuciscus cephalus*, where he observed that the numbers of *P. laevis* increased with the length of the fish host, and suggested that the increase was related to the absolute area of intestine available for parasite attachment. On the other hand, according to Walkey (1967), Hine and Kennedy (1974b), Muzzall (1980), and others intensity of infection varies proportionally with age of the host because older and larger hosts consume more food and, therefore, acquire more parasites than younger and smaller hosts.

In most fishes, the intensity of infection increases as age or size of the host increases and it would be expected to be limited by the size of available habitat in the intestine. Results obtained by various workers in the field tend to give conflicting conclusions; some show density-dependence, others do not. It is, therefore, important to support field data with laboratory experiments in order to clarify field patterns.

Other effects of crowding demonstrated by several workers are extension of the site occupied and reduced establishment, survival, growth, egg production, and fecundity (see review by Chappell and Pike, 1976). Burlingame and Chandler (1941) and Holmes (1961) have demonstrated, in laboratory infections of the rat, that *Moniliformis dubius* spread out, at high densities, into zones that have been sparsely occupied in lighter infections. This phenomenon has been demonstrated in other acanthocephalan species, for example *Echinorhynchus truttae* in *Salmo truttae* (Awachie, 1972) and *Pomphorhynchus laevis* in goldfish (Kennedy, 1972b).

Burlingame and Chandler (1941) reported that the establishment of secondary infections of *Moniliformis dubius* was inhibited by the presence of worms from primary infections and attributed this to competition for suitable sites of attachment within the "zone of viability", such that worms which failed to establish themselves in this zone or move into it early on in development failed to survive. In contrast, Awachie (1972) showed that, in experimental infections, the establishment of *Echinorhynchus truttae* in secondary and higher order infections was little affected by the presence of parasites established in earlier infections, and suggested that the difference between *E. truttae*, on the one hand, and *M. dubius* on the other, is probably due to the fact that *E. truttae*, unlike *M. dubius*, can establish and survive in all parts of the intestine.

Similarly, Brown (1986) demonstrated a density-dependent establishment and survival of *Pomphorhynchus laevis* in secondary infections in laboratory-infected rainbow trout. He showed that when pre-established parasites were small (less than 7 days old) and their numbers less than the carrying capacity of the infected host, then superimposed infections are possible. On the other hand, when the worms of the pre-existing infection were large and mature, the number establishing in superimposed infections decreased. In contrast, Kennedy (1972b, 1974) has demontrated that in laboratory infections in goldfish (in which there is little growth and no maturation of the parasites), there was no relationship between the rate of establishment of *Pomphorhynchus laevis* and the size or presence of an existing primary infection. Thus, the size or age of the worms in a primary infection has a big influence on establishment in secondary infections.

On the effect of crowding on growth (size), Burlingame and Chandler (1941) and Holmes (1961) demonstrated a significant decrease in the size of *Moniliformis dubius* and *Hymenolepis diminuta* under crowded conditions. In contrast, Brown (1986) showed that, in laboratory-infected rainbow trout, there was no significant difference in the mean individual wet weight of male and female *Pomphorhynchus laevis* recovered from fish originally given 5, 20, 50, or 100 parasites.

The number of gravid females may decrease under crowded conditions. Holmes *et al.* (1977) showed that in natural infections of *Coregonus clupeaformis* with *Echinorhynchus salmonis* there was a density-dependent regulation of egg production by the acanthocephalans in individual fish. They obtained a significant negative regression of the percentage of gravid females on intensity of infection. They, however, did not see any correlation in either *C. artedii* or *Oncorhynchus kisutch*.

High densities may, however, have some beneficial effects, especially in species requiring cross-fertilisation. Awachie (1966, 1972) found that most female *Echinorhynchus truttae* from the intestine of brown trout exposed to heavy infections bore young, developing acanthors which were free in the body cavity, whilst in control fish with low numbers of worms the females were only at the ovarian ball stage. He concluded that the initial presence of large numbers of worms in the intestine ensured earlier fertilisation and development of the eggs. Chubb (1964) found that, in grayling, roach and pike, relatively few female *Echinorhynchus clavula* had shelled acanthors, whilst in the eel the majority of the female worms contained shelled acanthors. He attributed the greater productivity in the eel to the higher concentration of worms in their intestine but, also, recognised that this could be due to a greater physiological compatibility with the eel.

The crowding effect has been related to competition for oxygen (Read, 1951), competition for carbohydrates (Read, 1959; Holmes, 1961; Roberts, 1961, 1966; and others), elaboration of inhibitors (Zavras and Roberts, 1985), interference with each others behaviour (Park, 1962) and, possibly, host immune response which results in loss of worms (Chappell and Pike, 1976). Host immune response has also been implicated in site extension. The antibody response of the host may render the normal site unsuitable for further occupation and, in doing so, initiate an emigration or extension of site (Brambell, 1965; Ogilvie, 1965; Connan, 1966; Panter, 1969), or degradation of the tissues in the site by earlier occupants (Shostak, 1986). No wholly satisfactory explanation has yet been provided for the crowding effect and it could be that different factors or a combination of factors are responsible for the observed effects in different systems.

Most of the investigations into host-parasite relations have involved separate studies on seasonal patterns, habitat specificity, and intraspecific crowding effects, the latter mainly in laboratory infections. It would be expected that in systems where very distinct and prominent seasonal patterns of intensity are observed, there might be seasonal changes in site occupied and some crowding effects. In this study of the *P. bulbocolli*-white sucker system, therefore, an attempt will be made to relate all three phenomena from field studies.

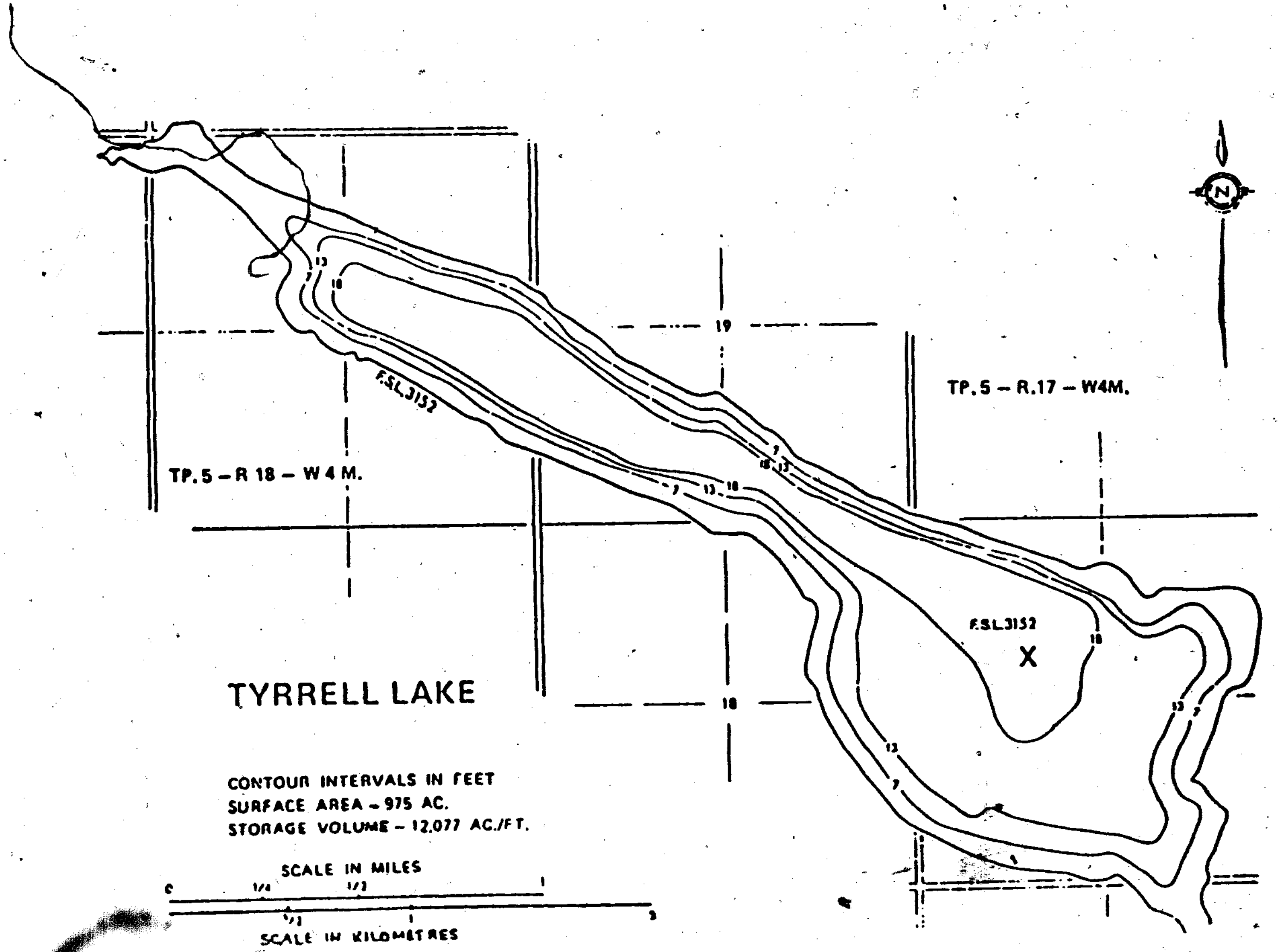
II. MATERIALS AND METHODS

A. STUDY SITE

Tyrrell Lake (Figure 1) is a natural lake situated approximately 52 km south-east of Lethbridge, Alberta, Canada (49° 23' N, 112° 15' W), in a semi-arid climate with an annual precipitation of about 300 mm. It occupies an area of 375 ha (975 acres), at an elevation of 960.4 m (3151 feet), with a mean depth of 3.8 m (12.4 feet) (Fitch, 1980). It is located within a shallow basin, surrounded by highly mineralised soil in an area with strong winds, warm summer temperatures and fluctuating water levels (Fitch,1980). Drainage from the lake is periodic so that it becomes a closed system with no outflow into the drainage system when water level is below 959.5 m (Fitch, 1980). The lake is unprotected from any winds and this allows for continuous circulation, resulting in in a fairly uniform temperature regime (Fitch, 1980). Maximum summer surface temperatures occur in July, the mean summer temperature being about 14°C with no apparent stratification. Dissolved oxygen concentrations fluctuate but there is, apparently, a low in mid-summer which may reach a critical level of less than 3.0 mg/l. Dissolved oxygen concentrations also fluctuate in winter and may reach low levels of less than 6.0 mg/l in some years (Fitch, 1980).

Tyrrell Lake is very saline, with sulphate (1235-5400 mg/l) and bicarbonate (177-882 mg/l) being the predominant anions, while chloride is of minor importance (35-185 mg/l). Sodium is the predominant cation (555-2500 mg/l); calcium and magnesium also occur in high concentrations (Fitch, 1980). The concentrations of these major chemical constituents follow a seasonal pattern, low in spring, increasing in summer and reaching a maximum in early autumn. TDS (total dissolved solids) range from 2500-8875 mg/l. Turbidity fluctuates between 2.6 and 15 m (Secchi disk depth), being high in spring, decreasing throughout summer and increasing again in autumn (Fitch, 1980).

Before the introduction of rainbow trout, *Salmo gairdneri*, in 1962, there were only white suckers, *Catostomus commersoni*, fathead minnows, *Pimephales promelas*, and brook sticklebacks, *Culaea inconstans*, in the lake. Occasional adults of five other species of fish,



GUR Map of Tyrrell Lake, the study area. X indicates the collection site. (Modified from Fitch, 1980) northern pike, *Esox lucius*; burbot, *Lota lota*; longnose sucker, *Catostomus catostomus*; lake chub, *Couesius plumbeus*; and lake whitefish, *Coregonus clupeaformis*, have been collected. Fitch (1980) concluded that they are probably migrants from the drainage system (i.e., they have not formed self-sustaining populations in the lake). Neotenic tiger salamanders, *Ambystoma tigrinum*, were also collected in all months during the course of this study. It has been suggested that the chemical composition of the lake is not suitable for the reproduction of the fish species, with the exception of the fathead minnows and brook sticklebacks (Fitch, 1980). Since 1985, when this study began, the only large species of fish that has been caught is the white sucker, confirming the suggestion that it is a permanent resident in the lake. That the others were found because of periodic and irregular movements into the lake is borne out by the collection (for the first time since 1985) of one large, uninfected whitefish, at a time when the water level was being raised with water from the surrounding drainage system.

Tyrrell Lake is eutrophic, with a high biological productivity; the total weight of benthic invertebrates is 61.29 g/sq. m. The zooplankton population is made up of copepods (*Diaptomus sicilis*, *Diaptomus nevadensis*, and *Acanthocyclops vernalis*), cladocerans (*Daphnia pulicaria*), ostracods and rotiferans, the latter two occurring only in small numbers. Benthic invertebrates are chironomid larvae, oligochaetes (*Tubifex*), amphipoda (*Hyallela azteca*), and fairy shrimps (*Branchinecta coloradensis*). Little is known about the phytoplankton of the lake. Aquatic vegetation is limited to a few species, predominantly *Potamogeton pectinatus*. Further details can be found in Fitch (1980).

B. INTERMEDIATE HOST

Monthly samples of the intermediate host, *Hyallela azteca*, were collected by sweeping with a small-meshed dip net in shallow areas, within 10m of the shoreline. They were transported to Edmonton in covered plastic buckets containing aerated lake water and, in the laboratory, gradually acclimatised to aerated, dechlorinated tap water by gradual dilution of the lake water over a period of two weeks. The amphipods were examined and classified as to sex, infected or uninfected, and reproductive condition of females (breeding or non-breeding).

C. DEFINITIVE HOST

The definitive host, white sucker (*Catostomus commersoni*), were collected with gill nets in July, 1985, and from May through September, 1986. The July, 1985, sample consisted of three age classes of fish, whilst the rest consisted of three-year old fish only. They were transported on ice and kept in the laboratory at 4°C for three days or less, depending on their number. Within this period each fish was tagged, its length and weight taken, the reproductive condition of females determined, and the alimentary tract, from oesophagus to anus, removed for parasite examination. A sample of scales was also taken from the left side of the body, just beneath the dorsal fin, of each fish and stored in 70% ethyl alcohol for age determination. In determining the age of each fish, five clean scales were spread out and pressed flat between two microscope slides held together with adhesive tape. The scales were allowed to dry overnight and then the number of growth rings was determined with the help of a microfiche reader.

D. STUDY OF PARASITES

The freshly removed intestine was uncoiled and divided into ten equal sections, section 1 being the anteriormost and section 10 the posteriormost (Figure 2). Each section was then opened up longitudinally, its average width taken, and a sample of gravid female *Pomphorhynchus bulbocolli* of various colour morphs (see below) removed, measured and kept in 0.7% saline for infection experiments. Each of the ten labelled sections of intestine from each fish was then placed in a labelled petri dish, covered, and stored in a freezer for examination at a later date. At the time of examination, the intestinal sections were thawed, placed in saline (to facilitate removal of the parasites without loss of the bulb and proboscis) for ten minutes, and the parasites were removed with the help of a pair of forceps, transferred into distilled water to stretch out, and each measured. The number of males, non-gravid females, and gravid females of each colour morph in each section was determined.

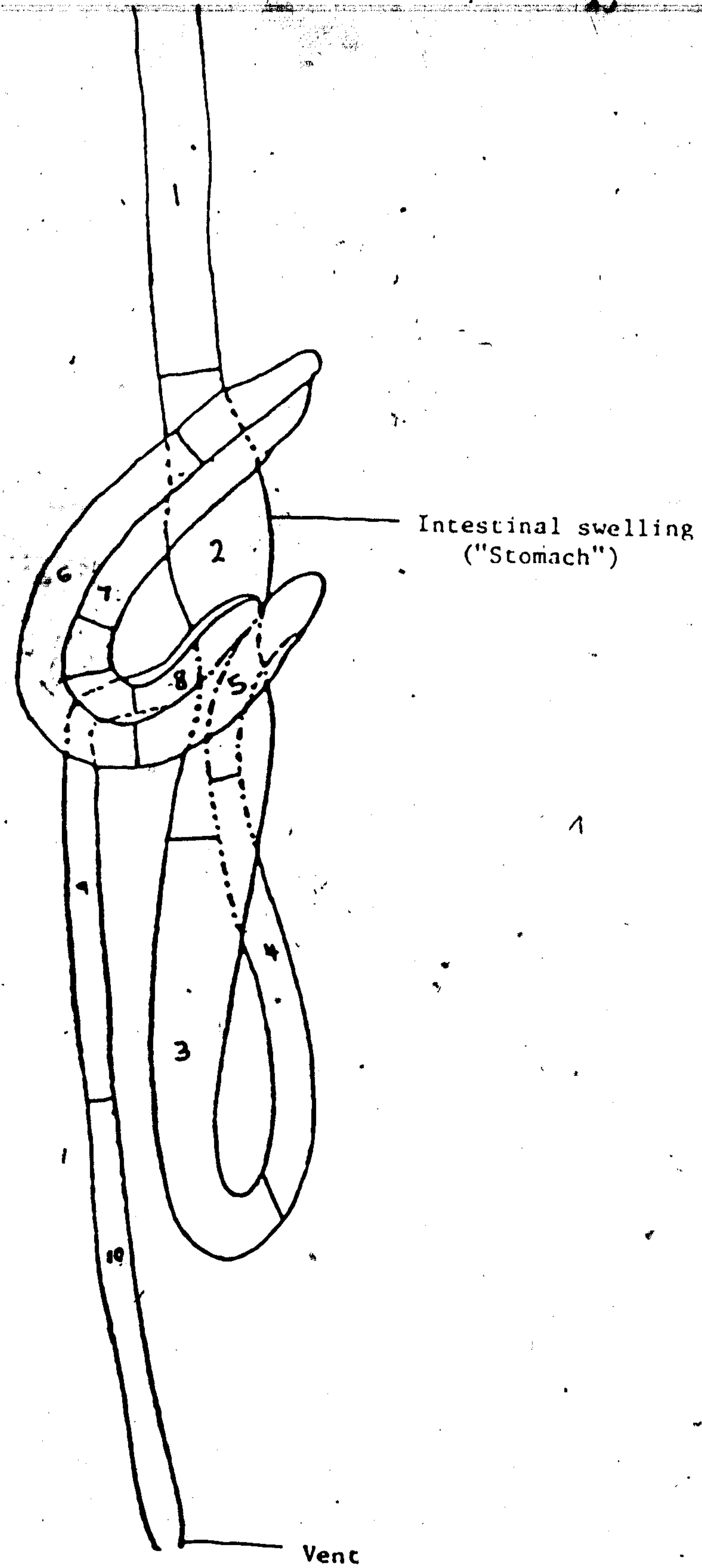


FIGURE 2: Intestine of white sucker showing sections 1-10. (Modified from Amin, 1975b)

Non-gravid females were classified as those without shelled eggs, and gravid females were those with shelled eggs. The maturity of males was not determined because the large numbers made histological examination impossible. Males and gravid females were arbitrarily divided into four categories based on their colour, i.e., cream, light yellow, yellow, and dark yellow. The types of food in the intestine were also noted.

E. INFECTION EXPERIMENTS

Study of the amphipods collected from Tyrrell Lake indicated that they could be used for infection experiments experiments immediately after collection because of the very low prevalence of infection, even after they were quarantined for weeks. Each freshly removed, live and unfrozen gravid female *P. bulbocolli* of known length, colour, and section was teased apart in 5ml of 0.7% saline, and the solution, containing eggs, was then added to finger bowls containing 100ml of dechlorinated tap water and about 50 amphipods which had been starved overnight. The amphipods were allowed to feed on the eggs overnight, after which they were washed free of eggs and transferred to large culture bowls containing dechlorinated tap water. At weekly intervals, samples were removed and dissected for larvae. The experiments were carried out in an environmental chamber at a temperature of 20°C.

Samples of eggs obtained from gravid females of known length, colour, and section and used in the infection experiments were stained in eosin and examined under the compound microscope. Approximately 1000 eggs were examined from each female worm. Eggs were classified into four groups, according to the presence or absence of shells and the extent to which nuclei were concentrated in the core of the embryo. The groups recognised were - Stage 1 (fertilised, but little development) through Stage 4 (shelled, with nuclei tightly packed in the core of the eggs) (Figure 3). The percentage of each type of egg present was then calculated.

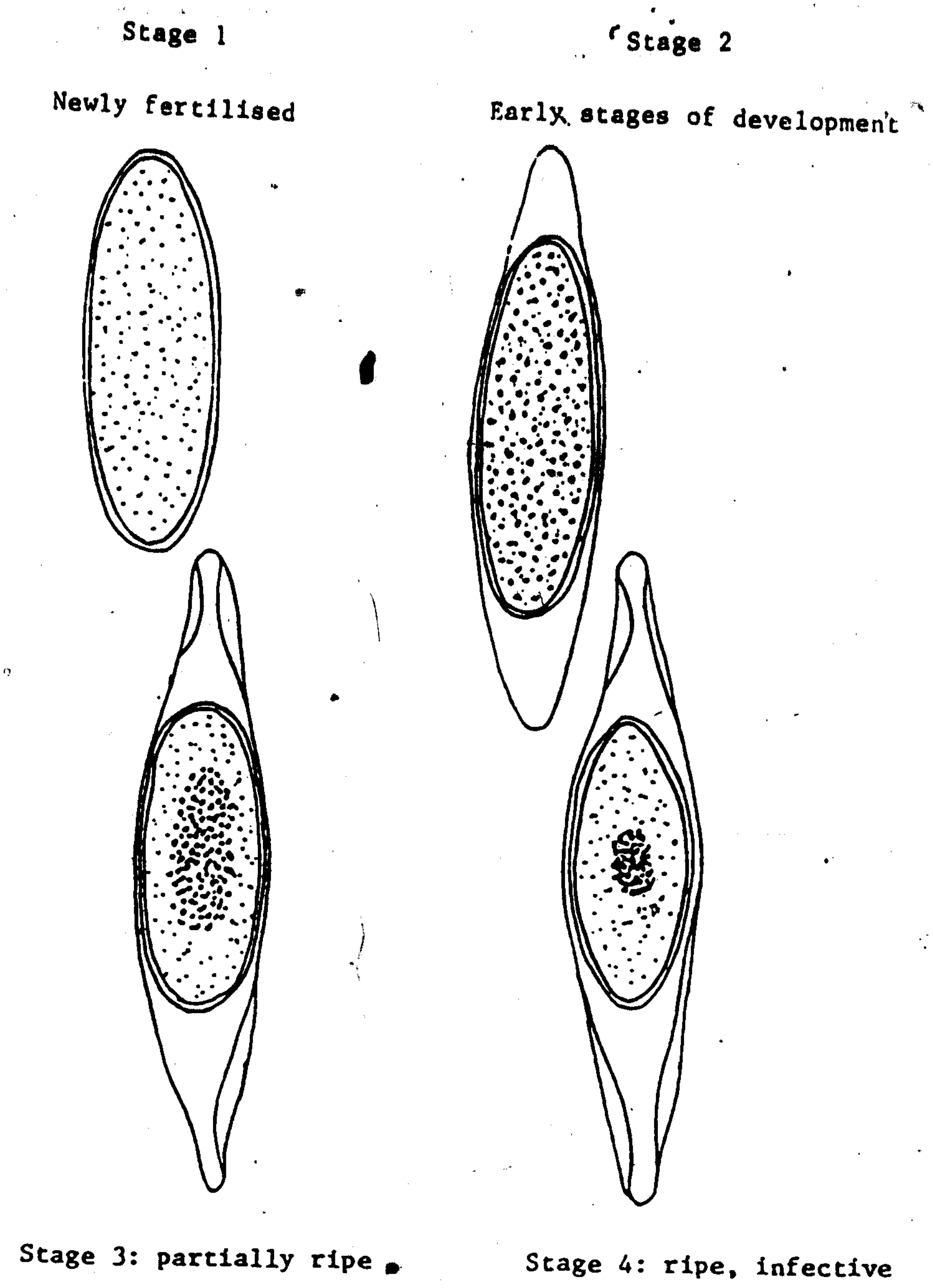


FIGURE 3: Stages of maturation of eggs of *Pomphorhynchus bulbocolli* in the intestines of white suckers.

F. STATISTICS

All data gathered were analysed statistically with analysis of variance and covariance, regression or chi-square, where appropriate, using programs in BMDP (Dixon, 1983), MIDAS (Fox and Guire, 1976), and SPSSx (Nei, 1975). A type 1 error of 5% was allowed. Variance / mean ratios were used to test for over-dispersion or aggregation and, where necessary, the data transformed. All statistical analyses involving percentages were arcsine-transformed. Welden and Slauson's (1986) interpretation of regression statistics was used, where the slope indicates the strength of the relationship and R-square indicates the relative importance of the relationship.

Some studies on the habitat specificity of intestinal helminth parasites involved a direct measurement of the precise location of the worms. In this study, however, it was impossible to measure the precise location of the worms because of the large numbers of worms encountered. The locations of the median, anteriormost and posteriormost individuals, as well as the range occupied by the worms, in each fish intestine were, therefore, calculated and expressed as percentages of the length of the intestine, using a FORTRAN program written by Drs. J. F. Addicott and J. C. Holmes, Department of Zoology, University of Alberta, Edmonton, Alberta, Canada. Within a section of the intestine, individuals were assumed to be equally spaced, with the space between the end of the section and the first (or last) individual assumed to be one-half of the distance between individuals. Statistical analyses on these distance measures were done with the programs mentioned above.

G. TERMINOLOGY

Samples of amphipods and white suckers were collected from Tyrrell Lake in only five (May through September), out of the twelve months. The term "season", as used in the following pages, refers to this period.

III. RESULTS

A. INTERMEDIATE HOST

The intermediate host, *Hyallela azteca*, was present in all summer months and samples of white suckers obtained during the summer all had large numbers of them in their intestines. No sampling for *H. azteca* was done in the winter, but rainbow trout in one samp obtained from Tyrrell Lake in January, 1982, had large numbers of them in their intestines. May-July, however, there were relatively more chironomid larvae and *Daphnia* in the intestines of the white suckers. These data suggest that the intermediate hosts are available and are fed upon all year round by the definitive hosts, but in spring and early summer (May-July) when water temperatures were rising and feeding increased, more chironomid larvae and *Daphnia* were eaten, compared to August-September. Other items of food found, occasionally and in small numbers, were algae and molluscs.

Prevalence (percentage of hosts infected) was very low in all months (Table 1). Only a single *P. bulbocolli* was found in each infected amphipod, but concurrent infections of larva *P. bulbocolli* and larvae of an unidentified polymorphid acanthocephalan were also found on rare occasions. There was no indication of a seasonal pattern of occurrence in the intermediat host (Table 1; 1986 data)(Chi-square=0.530, DF=4, Prob.=0.9705). Prevalence was, however, apparently higher in 1986 than in 1985.

Breeding of the intermediate host occurred during spring and summer. Both breeding (those carrying eggs or embryos in the brood pouch) and non-breeding females were found to be infected (Table 2). This suggests that, unlike some other acanthocephalans, *P. bulbocolli* does not sterilise the amphipods.

Table 1: Prevalence of *Pomphorhynchus bulbocolli* in the intermediate host, *Hyallela azteca*, by sex and month of collection. (- means unsexed)

Month	Male		Female		Total	Total
	Number Examined	Number Infected	Number Examined	Number Infected	Number Examined	Number Infected (%)
May '85	196	1	504	5	700	6 (0.9)
May '86	-	-	-		-	[illegible] (1.7)
Jun '85	399	1	613	7	1012	8 (0.8)
Jun '86	-	-	-		638	9 (1.4)
Jul '86	219	2	268	4	487	6 (1.2)
Aug '86	-	-	-		522	9 (1.7)
Sept '86	-	-	-		647	10 (1.5)

Table 2: Larval *Pomphorhynchus bulbocolli* in breeding and non-breeding female *Hyallela azteca*.

Month	Breeding		Non-breeding	
	Uninfected	Infected	Uninfected	Infected
May	201	1	298	4
June	367	4	239	3
July	146	2	118	2
Total	714	7	655	9

B. DEFINITIVE HOST

With the exception of two small, age 1^+ fish, all fish were infected in all months sampled. The statistical distribution of the numbers of worms in individual fish was markedly skewed (Figure 4). For each of the collections shown in Table 3, the variance was significantly larger than the mean, indicating an overdispersed (aggregated) distribution. Under such conditions, means and variances can be misleading. Therefore, all data on intensity (total number of worms per infected host) were log-transformed ($\log(x+1)$) and all statistical analyses were based on log-transformed data. This transformation did reduce the overdispersion considerably, as can be seen in Table 3.

Intensity of infection was found to be dependent on the sex and age of the host. Females harboured more worms than males (Table 4) so the sexes were kept separate in all statistical analyses involving intensity. The July sample included three age groups, whereas all other samples consisted of only three-year old fish; therefore, the July sample was used to determine the relationship between intensity of infection and age of hosts. The intensity of infection showed a significant regression on age ($p = 0.0007$), although the relationship was weak (slope=0.31 worms (log units) per year) and of little importance ($R^2 = 0.19$), mostly due to the similarity between two- and three-yea[illegible] fish (Table 5). There was no indication of age resistance in either sex. Because of the significant age effect only three-year old fish were used in subsequent analyses involving intensity.

Figure 5 illustrates size distribution of male, non-gravid and gravid female parasites. The size at conversion of non-gravid females (those without eggs) to gravid females (those with eggs) was approximately 10.0 mm. Copulation, as indicated by the presence of a cement cap, first occurred in this size group. It should be noted that those few non-gravid females in larger size classes were found mainly in unpreferred sites (see section D, Table 19).

Further growth and development of gravid females can be assessed by their size and the relative development of the eggs they contain. Both measures were strongly correlated with the colour of the worm, suggesting that dark worms were older than light-coloured worms. Cream-coloured worms were small, with the mean length of light yellow, yellow and dark

Table 3: Variance/mean ratios (V/M) of numbers (untransformed and log (x+1)-transformed) of *Pomphorhynchus bulbocolli* in individual fish in collections of white suckers.

			Untransformed			
Date	Sex	N	Mean	SD	V/M	Sig
May, '86	Both	6	157.7	96.2	58.7	HS[1]
Jun, '86	Male	24	147.0	107.0	77.8	HS
	Fem	36	191.8	152.8	121.7	HS
Jul, '86	Male	17	149.7	95.3	60.7	HS
	Fem	11	338.1	197.4	115.3	HS
Aug, '86	Male	16	69.8	53.5	41.1	HS
	Fem	34	119.2	93.6	73.1	HS
Sept, '86	Male	17	53.2	44.2	36.7	HS
	Fem	25	107.0	69.1	44.7	HS

[1] =$p<0.001$

Table 3 continued:

Log (x+1)-transformed

Date	Sex	N	Mean	SD	V/M	Sig
May, '86	Both	6	2.15	0.30	0.04	NS[2]
Jun, '86	Male	24	2.07	0.31	0.05	NS
	Fem	36	2.13	0.43	0.09	NS
Jul, '86	Male	17	2.09	0.29	0.04	NS
	Fem	11	2.45	0.31	0.04	NS
Aug, '86	Male	16	1.71	0.39	0.09	NS
	Fem	34	1.96	0.34	0.06	NS
Sept, '86	Male	17	1.60	0.37	0.09	NS
	Fem	25	1.94	0.32	0.05	NS

[2] = $p>0.05$

Table 4: Seasonal variation in number (log $(x+1)$-transformed) of *Pomphorhynchus bulbocolli* in male and female white suckers.

Month	Male Fish			Female Fish		
	Number of Fish	Log. No. of Worms		Number of Fish	Log No. of Worms	
		Mean	S.D.		Mean	S.D.
May	2	2.0	0.35	4	2.3	0.26
Jun	24	2.07	0.31	36	2.13	0.43
Jul	17	2.09	0.29	11	2.45	0.31
Aug	16	1.71	0.39	34	1.96	0.34
Sept	17	1.60	0.37	25	1.94	0.32

Table 4 continued:

Anova Table (log (x+1)-transformed data, May not included)

Source	SS	DF	MS	F	Prob
Month	5.7277	3	1.9092	15.19	0.0000
Sex	2.4529	1	2.4529	19.52	0.0000
MS	0.6465	3	0.2155	1.72	0.1657
Error	21.6120	172	0.1257		

Table 5: Mean numbers (log (x+1)-transformed) of ***Pomphorhynchus bulbocolli*** in various age groups of white suckers. (July sample only)

Age of Fish	Male Fish			Female Fish		
	N	Mean	SD	N	Mean	SD
1	6	1.17	0.96	3	1.96	0.33
2	8	2.07	0.34	12	2.32	0.29
3	17	2.09	0.29	11	2.45	0.31

Table 5 continued:

Least square regression of intensity of infection on age of white suckers. (log (x+1)-transformed intensity data from July sample only)

Source	SS	DF	MS	F	Prob.
Reg.	3.3036	1	0.0355	12.831	0.0007
Error	13.012	55	0.2366		
Total	16.047	56			
R=0.4349		R-Square=0.1892		SE=0.4864	
Variable	Partial	Coeff	S.E	T-Stat	Sig
Constant		1.3646	0.2148	6.3521	0.0000
Age	0.4349	0.3146	0.0878	3.5820	0.0007

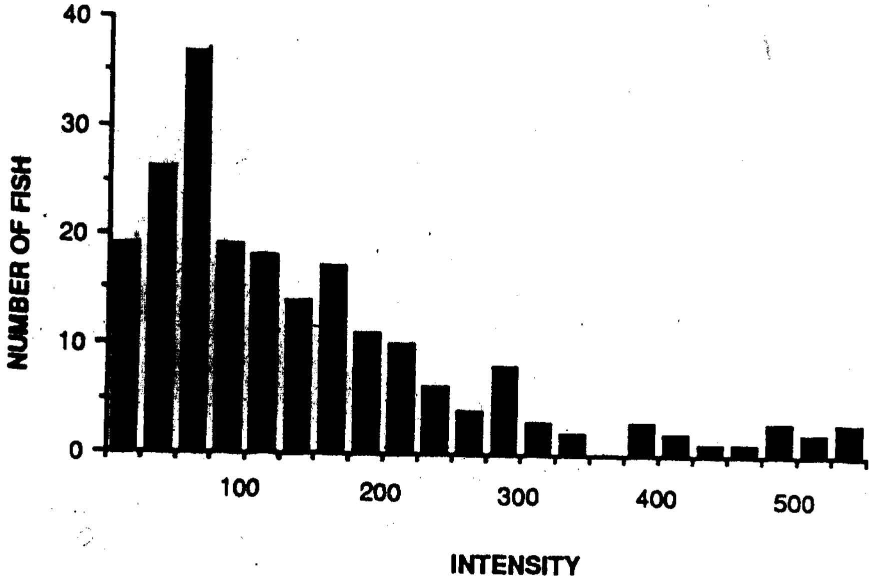


FIGURE 4: Distribution of numbers of *Pomphorhynchus bulbocolli* in individual white suckers.

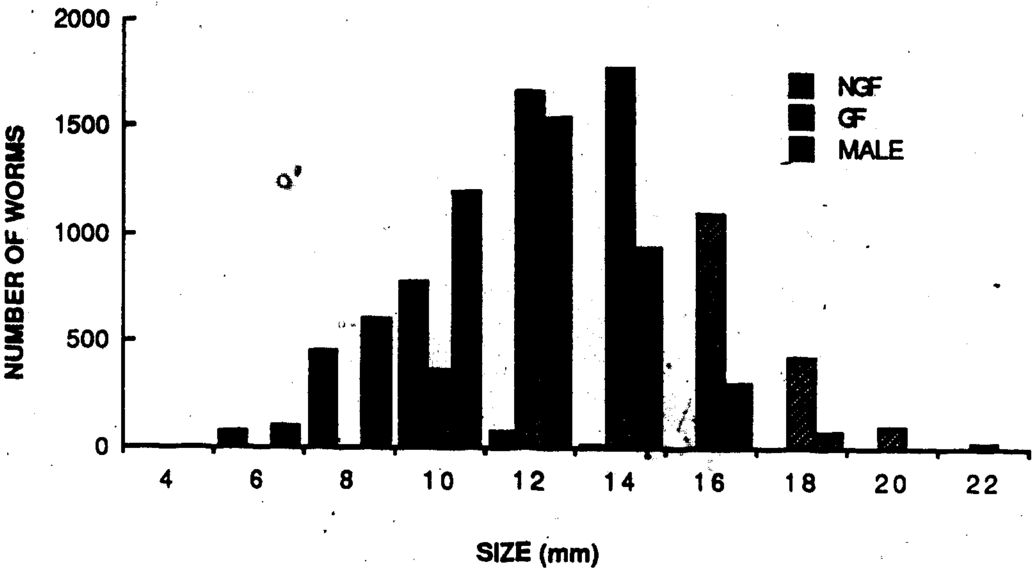


Figure 5: Size distribution of male, non-gravid (NGF) and gravid female (GF) *Pomphorhynchus bulbocolli* in white suckers. All data combined.

yellow worms increasing with the intensity of the colour (Table 6). Eggs were ~~relatively~~ undeveloped in cream-coloured worms, showed increasing development in light yellow and yellow worms, and fully developed, presumably ripe, infective eggs were found only in the dark yellow females (Table 7). (The sample size is small but the trend was strongly supported by non-quantitative observations made on all the specimens examined in the course of the study.) Only eggs from the dark yellow females gave successful infections of *Hyallela azteca* in the laboratory (Table 8).

C. SEASONAL PATTERNS

There was a clear seasonal pattern of intensity of infection. In both male and female fish, intensity was high from May through July, and decreased through August and September. Despite the variation in the data, this pattern was highly significant (Table 4).

There was also a clear pattern in invasion of new worms, as indicated by the number of small (up to 6.00 mm long) *P. bulbocolli*. Small worms were found in all months (including one winter sample of rainbow trout obtained from Tyrrell Lake in 1982). The numbers of small worms were low in mid-summer, but high in May and in September (Table 9). This pattern suggests invasion throughout the year, with lower invasion in mid-summer, possibly complicated by more rapid growth or more rapid elimination of incoming worms at the higher temperatures of mid-summer or a combination of these factors. The consumption of relatively few amphipods in mid-summer may also be a factor.

The correlations between the colour of a female, its size, and the development of its eggs, allows colour to be used as a measure of development in assessing the seasonal patterns of egg production and release. Preliminary analyses (analysis of covariance, using intensity as the covariate) indicated that the percentages o[illegible]ale, gravid females (GF), cream (C), light yellow (LY), yellow (Y), and dark yellow (DY) were highly variable among fish, but did not depend on the sex of the host, nor did any show significant relationships with intensity. The data can, therefore, be analysed with a simple one-way analysis of variance.

Table 6: Mean length (mm) of ***Pomphorhynchus bulbocolli*** of different colours in white suckers. All data combined. (Standard deviations in parentheses)

	Female Worms		Male Worms	
Colour of worm	Number of worms	Ave. L (mm)	Number of worms	Ave. L (mm)
Cream	1966	12.3 (0.07)	2305	9.8 (0.04)
Light Yellow	2523	13.5 (0.05)	1705	11.7 (0.05)
Yellow	253	14.9 (0.17)	88	13.1 (0.25)
Dark Yellow	28	16.9 (0.45)	11	13.5 (0.92)

Anova Table (Female worms)

Source	SS	DF	MS	F	Prob.
Between	3057.43	3	1019.14	169338	0.0000
Within	28.68	4766	0.0060		
Total	3086.12	4769			

Table 6 continued:

Anova Table (Male worms).

Source	SS	DF	MS	F	Prob.
Between	4066.53	3	1355.51	254687	0.0000
Within	21.85	4105	0.0053		
Total	4088.38	4108			

Table 7: Relationship between stage of maturation of acanthor (stages as in Figure 3) and colour of gravid female ***Pomphorhynchus bulbocolli*** in white suckers. 1000 eggs were examined for each worm. (Standard deviations in parentheses)

Colour of Worm	Month	Number of Worms	Ave. L. (mm)	% of eggs in stage 1	2	3	4
Cream	Jun	6	14.9 (3.2)	70 (15.2)	22 (10.6)	8 (5.6)	0
(C)	Aug	6	14.5 (3.0)	58 (10.3)	38 (10.9)	4 (3.2)	0
	Sept	7	14.8 (3.5)	73 (11.0)	24 (10.2)	4 (3.4)	0
	Total	19	14.7 (3.1)	67 (13.2)	28 (12.2)	5 (4.2)	0
Light	Jun	5	16.5 (2.4)	31 (5.8)	57 (7.0)	12 (9.5)	0
Yellow	Aug	6	16.4 (2.3)	36 (8.6)	58 (5.8)	8 (7.5)	0
(LY)	Sept	5	17.3 (4.2)	30 (16.8)	55 (4.5)	15.4 (16.1)	0
	Total	16	16.7 (2.9)	33 (10.8)	57 (5.6)	11.6 (11.1)	0

Table 7 continued:

Yellow	Jun	7	17.5 (2.8)	25 (15.9)	35 (16.0)	40 (28.6)	0
(Y)	Aug	3	18.4 (0.9)	28 (5.7)	48 (10.1)	24 (15.5)	0
	Sept	3	16.3 (2.5)	9 (5.1)	39 (22.7)	52 (18.0)	0
	Total	13	17.4 (2.4)	22 (14.0)	39 (16.2)	39 (24.6)	0
Dark	Jun	2	19.3 (0.3)	7 (9.2)	12 (11.3)	31 (22.6)	50 (43.1)
Yellow	Aug	1	18.4 (0.0)	17 (0.0)	29 (0.0)	34 (0.0)	20 (0.0)
	Total	3	18.9 (0.6)	12.0 (7.1)	20.5 (12.0)	32.5 (2.1)	35.0 (21.2)

Table 8: Proportion of *Hyallela azteca* infected by eggs from female *Pomphorhynchus bulbocolli* of different colours in white suckers.

Month	Colour of Worm			
	Cream	Light Yellow	Yellow	Dark Yellow
May	0/42	0/83	0/44	
June	0/105	0/45	0/119	22/68
Aug	0/111	0/89	0/39	0/32
Sept	0/103	0/99	0/74	
Total	0/361	0/316	0/276	22/100

Table 9: Seasonal occurrence of small (up to 6.0 mm) *Pomphorhynchus bulbocolli* in white suckers.

Month	Total No. of Fish	Proportion of Worms Mean (SD)	Log Number of Worms Mean (SD)	Proportion of Fish with Small Worms
May	6	0.038 (0.068)	0.56 (0.72)	.50
Jun	60	0.004 (0.011)	0.14 (0.29)	.23
Jul	28	0.001 (0.002)	0.04 (0.14)	.12
Aug	50	0.006 (0.013)	0.13 (0.25)	.26
Sept	42	0.012 (0.026)	0.19 (0.34)	.31

Table 9 continued:

Anova Table for percentage of small worms (arcsine-transformed).

Source	SS	DF	MS	F	Prob.
Between	0.0085	4	0.0021	5.8643	0.0002
Within	0.0654	181	0.0004		
Total	0.0739	185			

Anova Table for number of small worms (log-transformed).

Source	SS	DF	MS	F	Prob.
Between	1.4502	4	0.3626	4.1270	0.0032
Within	15.812	181	0.0878		
Total	17.263	185			

Gravid females (cream, light yellow and yellow phases) were found in all months, but ripe females (dark yellow colour) were found only in June, July, and August (Table 10). Although no samples of white sucker were obtained from Tyrrell Lake in winter, those obtained from Muriel Lake, Alberta, in February had non-gravid, cream, light yellow and yellow (but no dark yellow) females, as did rainbow trout obtained from Tyrrell Lake in January, 1982. The number of gravid females (GF) (used as a measure of egg production) (Table 11) and dark yellow females (DY) (used as an index of egg release) (Table 12) depend on season, both being low in June, reaching a high in July, and decreasing the rest of the summer (Figure 6). Dark yellow females formed only a small proportion of the females, suggesting that either only a small proportion of the females actually release eggs or dark yellow females complete their development rapidly and have a short life span. Thus invasion and egg production occur all year round, including winter, whilst complete egg development appears to be limited to the summer period.

Table 13 shows a comparison of the survival or development indices among months, and the statistical analyses indicate that there are no significant differences. However, there seem to be a pattern. The cream:light (C:LY) yellow ratio indicate that in June and July loss or development were about the same. Between July and August the ratio increased, suggesting either a loss of light yellow worms or less conversion of cream worms into light yellow worms; the decrease in intensity of infection suggests that there was a net loss of light yellow worms. Between August and September there was an increase in the ratio, suggesting increased development into light yellow worms or a loss of cream worms; the decrease in intensity of infection during this period suggests there was a net loss of cream worms. The light yellow:yellow ratio (LY:Y) decreased considerably between June and July, suggesting good development into yellow worms or a loss of light yellow worms; the increase intensity of infection suggests that there was a net development into yellow worms. The ratio returned to high values in August and September, suggesting either a loss of yellow worms or poor development into yellow worms; the decrease in intensity of infection during this period suggests there was a net loss of yellow worms. It seems, therefore, that between July and

Table 10: Seasonal patterns of development of *Pomphorhynchus bulbocolli* in white suckers. (Refer to Table 7 for abbreviations; standard deviations parentheses)

Month	No. of Fish	% C	% LY	log Y	% Y	log DY	% DY
May	6	0.65	0.31	1.1	0.05	0	0
		(0.22)	(0.25)	(0.7)	(8.1)		
Jun	60	0.67	0.46	0.21	0.007	0.03	0.0006
		(0.39)	(0.33)	(0.31)	(0.015)	(0.11)	(0.0024)
Jul	28	0.58	0.47	0.46	0.028	0.21	0.0083
		(0.31)	(0.25)	(0.57)	(0.048)	(0.35)	(0.0199)
Aug	50	0.73	0.45	0.08	0.004	0.02	0.0009
		(0.44)	(0.40)	(0.19)	(0.014)	(0.07)	(0.0043)
Sept	42	0.52	0.59	0.13	0.011	0	0
		(0.38)	(0.37)	(0.23)	(0.040)		
F		2.5748	1.5266	9.3023	4.5044	12.521	7.0210
Prob		0.0555	0.2093	0.0000	0.0045	0.0000	0.0002

Table 10 continued: GF and NGF represent gravid and non-gravid females, respectively.

Month	N	log GF	% GF	log NGF	% NGF	log Small	% Small	% Male
May	6	1.71	0.48	1.00	0.10	0.60	0.04	0.41
		(0.10)	(0.09)	(0.64)	(0.08)	(0.72)	(0.07)	(0.07)
Jun	60	1.73	0.46	1.13	0.14	0.14	0.004	0.44
		(0.37)	(0.13)	(0.57)	(0.10)	(0.29)	(0.011)	(0.07)
Jul	28	1.94	0.55	0.73	0.04	0.04	0.0005	0.44
		(0.35)	(0.09)	(0.54)	(0.05)	(0.14)	(0.002)	(0.07)
Aug	50	1.59	0.54	0.73	0.07	0.13	0.006	0.43
		(0.36)	(0.10)	(0.53)	(0.06)	(0.25)	(0.013)	(0.09)
Sept	42	1.51	0.55	0.63	0.06	0.19	0.012	0.43
		(0.35)	(0.13)	(0.50)	(0.06)	(0.34)	(0.026)	(0.10)
F		9.6692	7.0056	6.7982	10.353	4.1270	5.8643	0.3709
Prob		0.0000	0.0002	0.0000	0.0000	0.0032	0.0002	0.7741

Table 11: Occurrence of gravid female (GF) ***Pomphorhynchus bulbocolli*** in male and female white suckers in different months.

(Percentages are arcsine-transformed; standard deviations in parentheses)

	Male Fish			Female Fish		
Month	N	% GF	Log No.	N	% GF	Log No.
June	24	0.40 (0.15)	1.63 (0.25)	36	0.49 (0.11)	1.80 (0.42)
July	17	0.55 (0.11)	1.81 (0.28)	11	0.54 (0.05)	2.16 (0.34)
Aug	16	0.53 (0.11)	1.42 (0.36)	34	0.54 (0.10)	1.67 (0.33)
Sept	17	0.53 (0.14)	1.30 (0.35)	25	0.56 (0.13)	1.65 (0.29)

Anova Table of percent GF (arcsine-transformed).

Source	SS	DF	MS	F	Prob
Month	0.3374	3	0.1125	8.07	0.0000
Sex	0.0383	1	0.0383	2.75	0.0993
MS	0.0720	3	0.0240	1.72	0.1645
Error	2.3981	172	0.0139		

Table 11 continued:

Anova Table of number of GF (log (x+1)-transformed).

Source	SS	DF	MS	F	Prob.
Month	4.8633	3	1.6211	14.44	0.0
Sex	3.0792	1	3.0792	27.42	0.0
MS	0.2733	3	0.0911	0.81	0.4892
Error	19.3156	172	0.1123		

Table 12: Occurrence of dark yellow (DY) female *Pomphorhynchus bulbocolli* in male and female white suckers in different months. (Standard deviations in parentheses)

Month	Sex of Fish	Total No. of Fish	No. with DY Worms	Log No. DY Worms	% of Total Worms
May	Male	2	0	0	0
	Female	4	0	0	0
June	Male	24	3	0.0450 (0.1251)	0.0002 (0.0007)
	Female	36	0	0	0
July	Male	17	7	0.1394 (0.2885)	0.0012 (0.0028)
	Female	26	2	0.1444 (0.2792)	0.0012 (0.0026)
Aug	Male	16	2	0.0376 (0.1028)	0.0002 (0.0004)
	Female	34	0	0	0
Sept	Male	17	0	0	0
	Female	25	0	0	0

Table 12 continued:

Anova Table for number of DY females (log (x + 1)-transformed).

Source	SS	DF	MS	F	Prob
Between Months	0.7153	3	0.2385	9.7555	0.0000
Within	5.0107	205	0.0244		
Total	5.7260	208			

Anova Table for percentage of DY females (arcsine-transformed).

Source	SS	DF	MS	F	Prob.
Between Months	0.0001	3	0.000019	9.0723	0.0000
Within	0.0004	205	0.000002		
Total	0.0005	208			

Table 13: Comparison of the development and survival indices of *Pomphorhynchus bulbocolli* in white suckers among months.

(Standard deviations in parentheses.)

Index	Month	Number of Fishes	Mean Ratio
C:LY	June	57	3.8 (9.1)
	July	55	3.8 (10.1)
	Aug	45	5.0 (11.2)
	Sept	41	2.5 (5.7)
F=0.4977		Prob=0.6843	
LY:Y	June	24	53.0 (64.4)
	July	24	21.0 (26.6)
	Aug	9	43.2 (41.9)
	Sept	12	40.6 (32.0)
F=1.9936		Prob=0.1236	

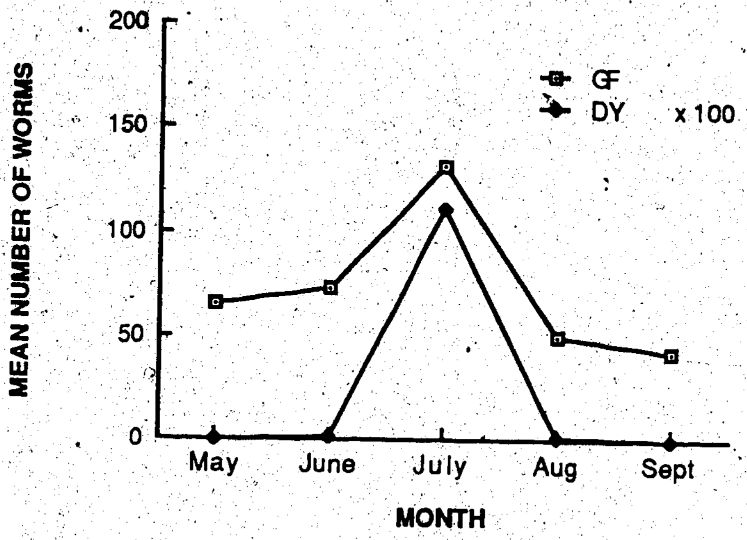


Figure 6: Seasonal pattern of egg production (gravid females, GF) and egg release (dark yellow females, DY).

August when there was a drastic drop in the intensity of infection there was a loss of light yellow, yellow, and dark yellow worms.

Males were smaller than female worms, and disappeared at a smaller size than females (Figure 5). In old acanthocephalan populations [illegible] some species, females occur in higher proportions than males, suggesting earlier [illegible] males (Amin, 1986, 1987a; Valtonen, 1980; and others). To test this, the male to female ratio was compared among the various colour morphs; the results (Table 14) indicated that the male to female ratio decreased significantly with increasing colour intensity (Chi-square=141.408, DF=4, p=0.0000). However, the percentage of males did not decrease in fish taken in late summer (Table 15), suggesting a high turnover of males.

Table 14: Male:female ratios (M:F) of *Pomphorhynchus bulbocolli* of different colours in white suckers. All data combined.

Colour of Worm	No. of Males	No. of Females	M:F Ratio
Cream	7364	9113	0.81
LY	4856	7333	0.66
Y	121	374	0.32
DY	16	48	0.33

Table 15: Seasonal variation in percent (arcsine-transfored) of male *Pomphorhynchus bulbocolli* in male and female white suckers. (Standard deviations in parentheses)

Month	Male Fish		Female Fish	
	N	Mean	N	Mean
May	2	0.43 (0.10)	4	0.45 (0.10)
June	24	0.44 (0.08)	36	0.45 (0.06)
July	11	0.48 (0.07)	17	0.42 (0.06)
Aug	16	0.44 (0.10)	34	0.43 (0.08)
Sept	17	0.46 (0.12)	25	0.42 (0.08)

Table 15 continued:

Anova Table (arcsine-transformed).

Source	SS	DF	MS	F	Prob
Month	0.0067	3	0.0022	0.33	0.8019
Sex	0.0003	1	0.0003	0.04	0.8434
MS	0.0374	3	0.0125	1.86	0.1389
Error	1.1560	172	0.0067		

D. HABITAT SPECIFICITY

Figure 7 shows the overall distribution of worms along the length of the intestine. About 83% of the worms (all age and sex categories combined) were concentrated in the 60 - 80% region (sections 7 and 8), indicating that this region was preferentially occupied.

For statistical analyses, the location of the medianth, anteriormost and posteriormost individuals, and the range occupied, in individual fish, were used. The age of the host had an effect on the location of the medianth and last individuals, but not on the first individual or the range occupied (Table 16). The medianth individual was located more anteriad in older fish relative to 1+ fish, possibly because more worms were found in older fish. The sex of the host was found to influence the location of the medianth and anteriormost individuals and the range; the median and anterior positions in female fish were located more anterior relative to male fish (Table 17), again possibly because female fish harboured more worms than male fish. (See section on crowding below for a more complete discussion.)

When the distributions of small worms, males, non-gravid, and gravid females were compared, the locations of the medianth individual were found to be the same (Table 18); all age and sex categories of worms preferentially occupied sections 7 and 8. There was significant variation in the anterior and posterior positions, and in the range occupied (Table 18); most of this variation appeared to be associated with the small worms, which occurred in small numbers. There was no evidence for any migration of worms from one area of settlement to an area of maturation.

However, comparison of the relative proportions of small, recently acquired worms, non-gravid and gravid females among sections (as measured by the percentage among all worms in the section) showed that the relative proportions of small worms was low in section 7 through 9, about twice as high in sections 4 through 6, and almost four times as high in section 10 (Figure 8). The proportion of non-gravid females was lowest in sections 7 and 8, increasing both anteriorly and posteriorly, whilst the proportion of gravid females, on the other hand, was highest in sections 7 and 8, decreasing anteriorly and, especially, posteriorly

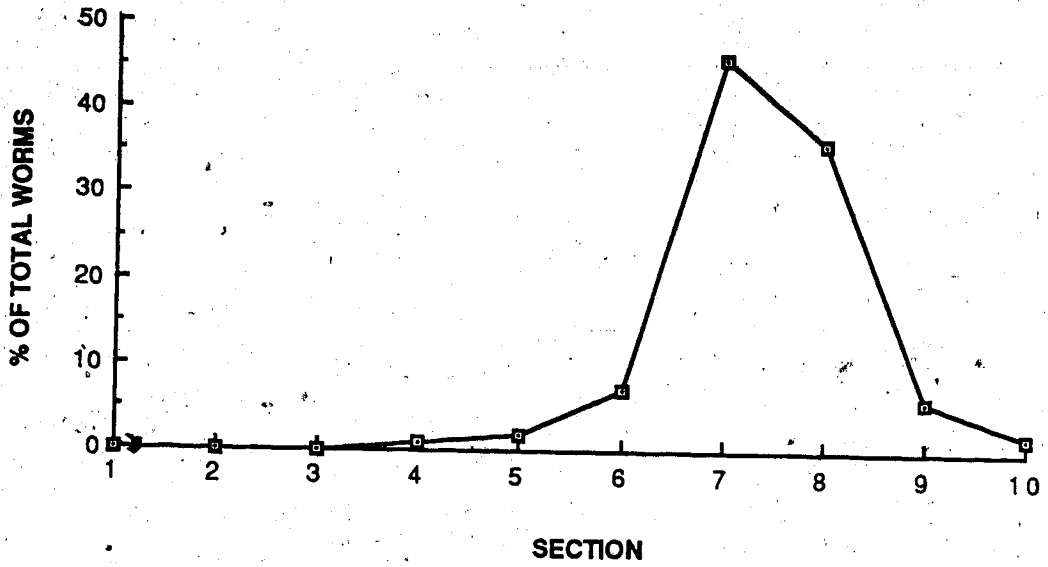


FIGURE 7: Overall distribution of *Pomphorhynchus bulbocolli* among intestinal sections of white suckers.

Table 16: Location (expressed as percent of intestinal length) of *Pomphorhynchus bulbocolli* in various age classes of white suckers. (July sample only; standard deviations in parentheses)

Age of Fish (yrs)	Gut Length (mm)	Mean Intensity (Log)	Mean Median Position	Mean Anterior Position	Mean Posterior Position	Mean Range
1	65.4	1.43	74.17	49.18	98.71	49.53
	(12.5)	(0.86)	(2.48)	(15.16)	(3.30)	(15.74)
2	75.3	2.22	71.20	48.76	95.81	47.05
	(8.5)	(0.32)	(2.87)	(9.77)	(5.95)	(13.63)
3	85.3	2.23	70.14	43.84	99.81	55.97
	(12.5)	(0.34)	(3.35)	(15.80)	(0.16)	(15.85)
DF		2, 54	2, 54	2, 54	2, 54	2, 54
F		11.33	5.88	0.95	6.72	2.16
Prob		0.0001	0.0049	0.3942	0.0025	0.1249

Table 17: Location (expressed as percent of intestinal length) of *Pomphorhynchus bulbocolli* in male and female white suckers. (Standard deviations in parentheses)

Sex of Fish	Gut Length (mm)	Mean Intensity (Log)	Mean Median Position	Mean Anterior Position	Mean Posterior Position	Mean Range
Male	80.6	1.85	69.59	44.36	96.09	51.08
	(9.3)	(0.48)	(4.62)	(13.00)	(6.67)	(15.46)
Female	92.3	2.08	67.82	39.33	96.14	56.81
	(11.1)	(0.37)	(3.90)	(12.50)	(5.62)	(14.82)
DF		1, 207	1, 207	1, 207	1, 207	1, 207
F		14.68	9.02	7.92	0.003	5.84
Prob.		0.0002	0.0030	0.0052	0.9561	0.0166

Table 18: Location (expressed as percent of intestinal length) of age, sex categories of *Pomphorhynchus bulbocolli* in white suckers. (Standard deviations in parentheses).

Worm	Prevalence (%)	Mean Intensity (Log)	Mean Median Position	Mean Anterior Position	Mean Posterior Position	Mean Range
Male	209/209	1.62	68.2	54.3	82.0	27.8
	(100)	(0.42)	(4.8)	(9.3)	(6.5)	(11.8)
NGF	209/209	0.81	68.6	56.3	80.6	24.3
	(100)	(0.57)	(6.1)	(9.8)	(8.0)	(12.4)
GF	209/209	1.68	68.1	54.9	80.8	25.9
	(100)	(0.43)	(5.3)	(9.1)	(6.5)	(10.7)
Small	47/209	0.58	69.1	60.1	76.7	16.6
	(22.5)	(0.25)	(10.5)	(13.2)	(13.1)	(17.1)
DF		3, 670	3, 670	3, 670	3, 670	3, 670
F		62.41	0.59	5.59	6.87	12.37
Prob		0.0000	0.6193	0.0009	0.0002	0.0006

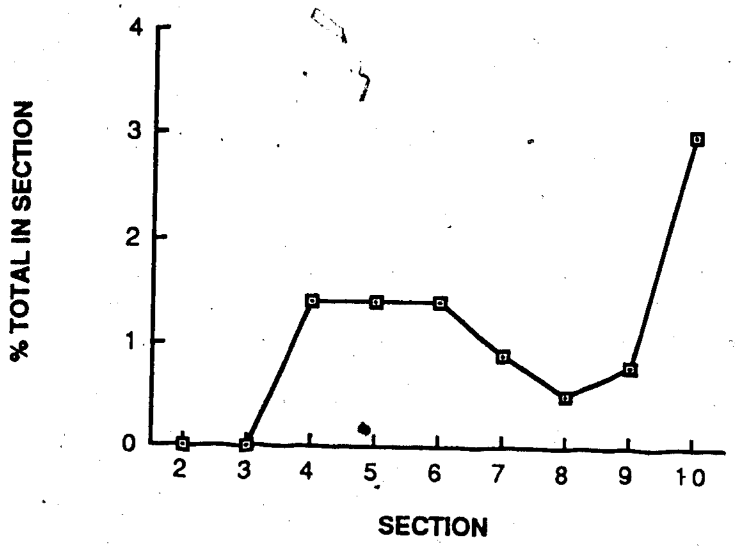


FIGURE 8: Relative distribution of small *Pomphorhynchus bulbocolli* along the length of the intestine of white suckers.

(Figure 9). Thus, small worms and non-gravid females were relatively more abundant in the unpreferred, less populated sites, whilst gravid females were more abundant in the preferred, more heavily populated sites. These patterns suggest either that establishment is low in already heavily populated areas or that growth, egg production or reproductive activity is low in the less populated areas. The significance of crowding will be covered below. However, large (10.1 - 12.0mm) females, which would be expected to be fertilised but were not, occurred mainly in the 80-100% region, sections 9 and 10 (Table 19); this suggests that this region may not be as suitable an environment. The presence of males of average size in the 80 - 100% region in the fishes with these females suggests that a complete absence of males was not responsible for the females not being fertilised; however, the distances separating male and female may have prevented copulation.

Unlike in other analyses, all measures of the distribution of the various colour morphs differed significantly (Table 20). The medians of dark yellow and yellow worms were located further anterior than those of cream and light yellow worms; in addition, these older worms were relatively more concentrated in section 7 (Figure 10). Although, on average, the yellow and dark yellow worms did not extend as far anteriorly as the cream and light yellow worms (Table 20), dark yellow worms did occur as far anteriorly as section 3 (Figure 10), indicating that the anterior portions are potentially suitable habitats. Cream worms reach furthest posteriorly, and dark yellow worms the least posteriorly. In fact, the older and more mature yellow and dark yellow worms were completely absent from sections 9 and 10 (Figure 10). The net result of these distributions was that the range occupied was greatest for cream worms, and more restricted for yellow and dark yellow worms (in part, due to small populations).

There was a significant variation in three of the four measures (all except range) with season, but there was no apparent trend (Table 21). At high intensities (May through July), the worms were concentrated in sections 7 and 8, with not much spread, but, contrary to expectation, at low intensities (August through September), they were less concentrated in sections 7 and 8 (Figure 11).

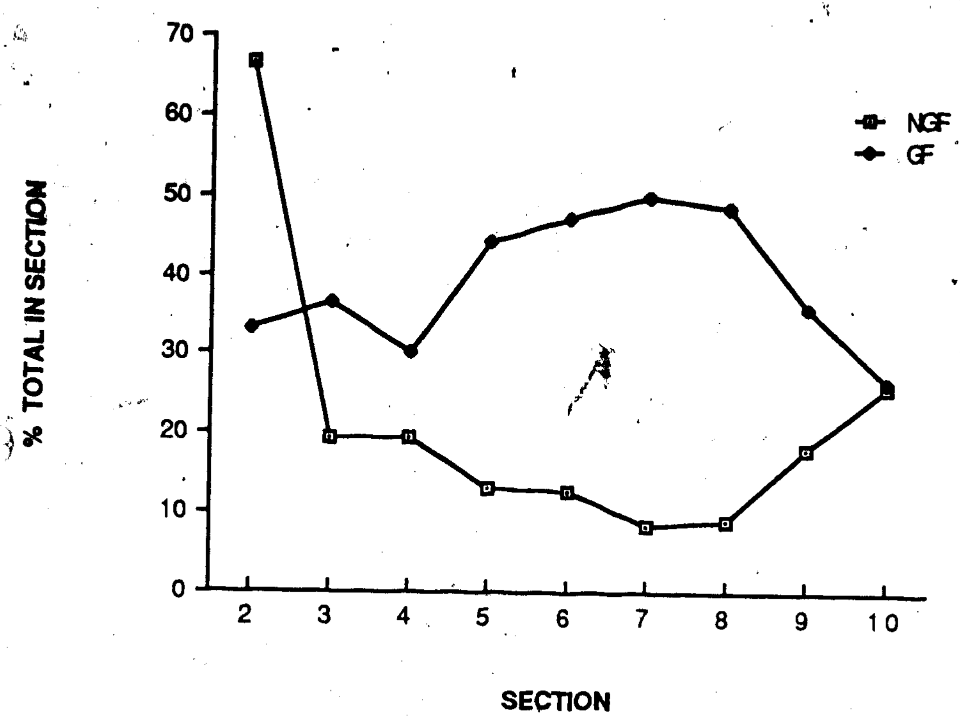


FIGURE 9: Relative distribution of non-gravid (NGF) and gravid (GF) female *Pomphorhynchus bulbocolli* among sections of the intestines of white suckers.

Table 19: Distribution of non-gravid female *Pomphorhynchus bulbocolli* in the intestine of white suckers.

Size	Section of Intestine								
(mm)	2	3	4	5	6	7	8	9	10
6.1-8.0	0	1	10	19	45	177	124	41	31
8.1-10.0	0	4	16	19	70	277	274	76	44
10.1+	0	0	1	4	8	7	7	47	20

Table 20: Location (expressed as of percent [illegible]nal length) of the various colour morphs of *Pomphorhynchus bulbocolli* in white suckers. (Standard deviations in parentheses)

Colour of Worm	Prevalence (%)	Mean Intensity (Log)	Mean Median Position	Mean Anterior Position	Mean Posterior Position	Mean Range
Cream	204/209	1.67	70.0	55.9	87.3	31.3
	(97.6)	(0.51)	(6.8)	(11.7)	(7.8)	(14.5)
LY	200/209	1.59	[illegible]	54.1	78.0	23.9
	(95.7)	(0.50)	(5.0)	(9.6)	(7.0)	(11.9)
Y	69/209	0.67	65.3	58.3	71.1	12.9
	(33.0)	(0.40)	(4.7)	(8.0)	(6.8)	(10.4)
DY	21/209	0.54	63.3	59.0	67.1	8.2
	(10.0)	(0.26)	(7.4)	(8.0)	(8.7)	(7.4)
DF		3, 490	3, 490	3, 490	3, 490	3, 490
F		20.67	25.79	4.01	130.94	54.14
Prob		0.0000	0.0000	0.0077	0.0000	0.0000

Table 21: Location (expressed as percent of intestinal length) of *Pomphorhynchus bulbocolli* in white suckers in different months. (Standard deviations in parentheses)

Month	Prev-lence (%)	Mean Intensity (Log)	Mean Median Position	Mean Anterior Position	Mean Posterior Position	Mean Range
June	60/60	2.24	69.64	40.59	95.93	55.34
	(100)	(0.38)	(3.04)	(11.71)	(6.15)	(14.49)
July	55/57	2.29	71.15	46.41	98.23	51.83
	(96.5)	(0.54)	(3.32)	(13.86)	(4.12)	(15.40)
Aug	50/50	1.88	65.15	39.04	94.52	55.49
	(100)	(0.37)	(4.16)	(11.64)	(6.80)	(114.80)
Sept	42/42	1.80	67.58	38.84	95.42	56.65
	(100)	(0.37)	(4.30)	(13.28)	(6.65)	(10.4)
DF		3, 205	3, 205	3, 205	3, 205	3, 205
F		6.47	26.46	4.22	3.81	0.96
Prob		0.0003	0.0000	0.0063	0.0110	0.4102

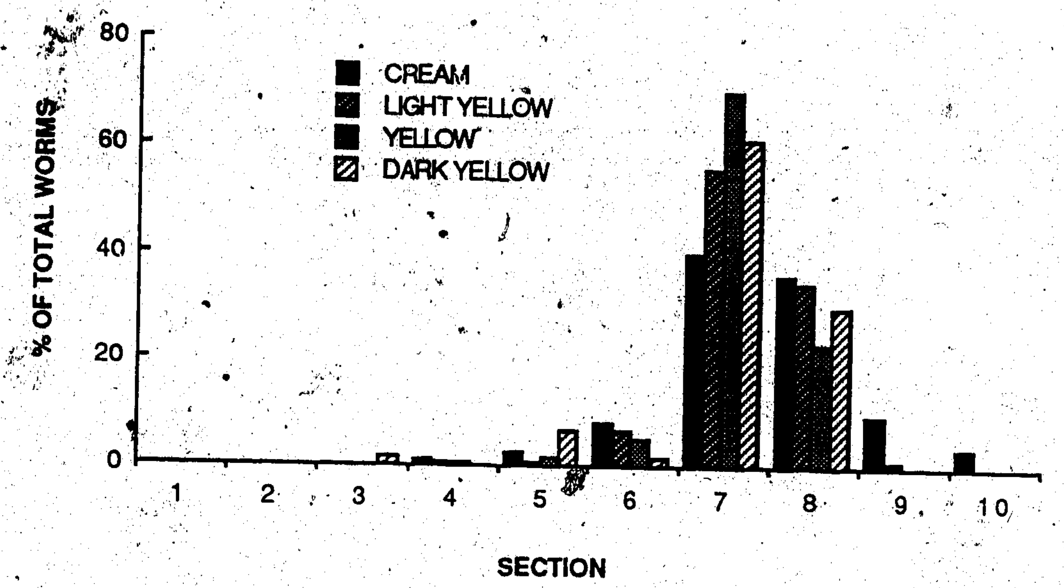


FIGURE 10: Distribution of colour morphs of *Pomphorhynchus bulbocolli* along the length of the intestine of white suckers. All data combined.

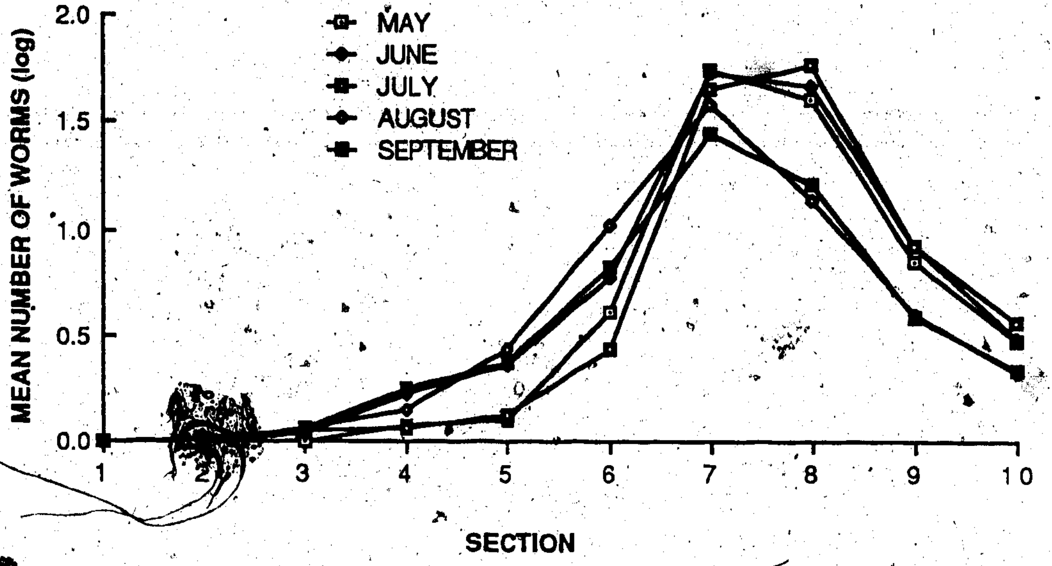


Figure 11: Distribution of *Pomphorhynchus bulbocolli* among sections of the intestine of white suckers in different months.

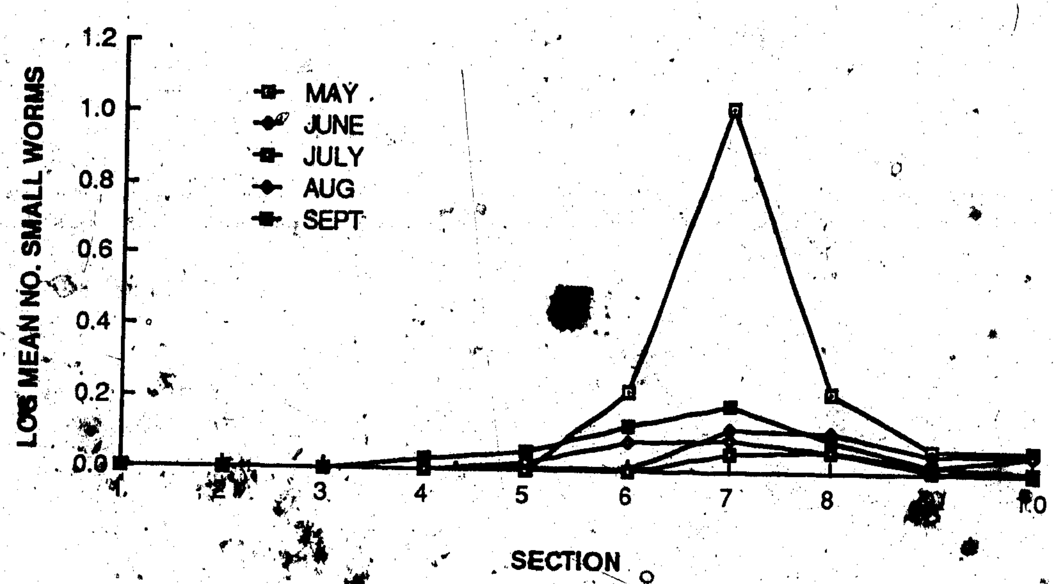


FIGURE 12: Distribution of small *Pomphorhynchus bulbocolli* among sections of the intestine of white suckers in different months.

The seasonal patterns of invasion and loss of worms may be responsible for the observed distribution. The loss of older worms was primarily from the dense populations in sections 7 and 8 (note changes between May through July and August and September (Figure 11), whereas establishment was more evenly spread through sections 6-8 (Figure 12), the net result being a small change in the distribution of worms without any appreciable change in the preferred sites.

To determine whether or not there was an equal development of worms among sections, the ratio of cream to light yellow worms was compared among months (Figure 13). In May, the proportion of cream-coloured wor[illegible]ections [illegible] and 10 was low, and roughly equivalent to that in the other parts of the intes[illegible] near the end of the invasion period, there were high proportions of cream-colo[illegible]orms in sections 9 and 10, whereas the proportions in the [illegible]ons were low and showed no differences. In August, when invasion recommence[illegible]rtion of cream-coloured worms in section 10 was low but built up again, to a high[illegible]ptember, the proportions in the other sections remaining virtually unchanged. This pattern, along with the presence of relatively few light yellow worms in this region, suggests that relatively more young worms were lost from the 80 - 100% region, and that worms do not live long enough to attain egg-releasing age in this portion of the intestine. The light yellow:yellow ratio was higher in the preferred sites, and decreased anteriorly, suggesting that survival or development to the yellow stage is poorer in the preferred sites, contrary to expectation (Figure 14).

Table 22 shows that the size of the worms varies significantly between sections. Two observations can be made, despite the absence of any trend across sections. First, non-gravid females in sections 3, 9 and 10 were larger, probably due to the occurrence of the relatively high proportions of large, unfertilised females in them. Second, other categories of worms were, generally smaller in section 10.

In summary, all age and sex categories of worms were concentrated in sections 7 and 8, irrespective of season. Three lines of evidence suggest that the 80-100% region of the intestine is not a suitable habitat. Relatively more large, unfertilised females, which would be

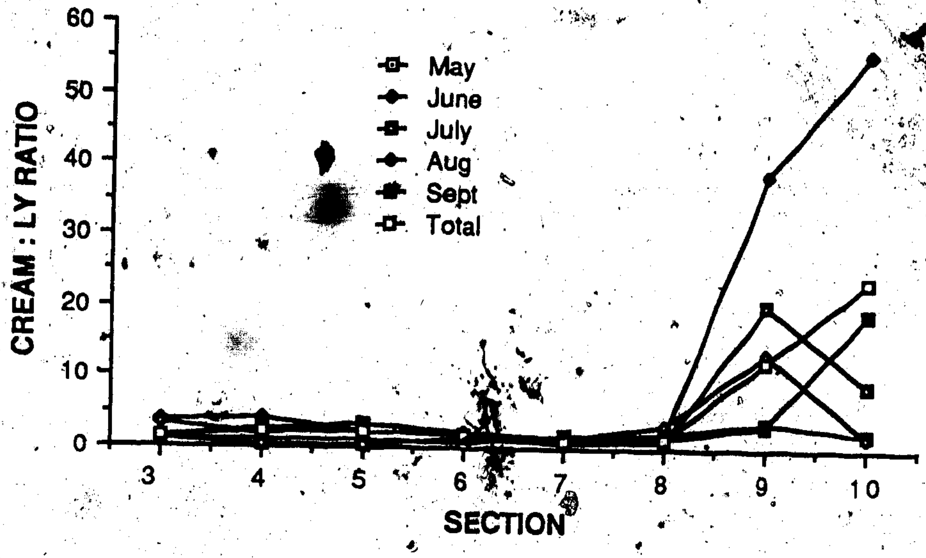


Fig 13: Cream : Light Yellow (LY) ratios of *Pomphorhynchus bulbocolli* among sections of the intestine of white suckers in different months.

Table 22: Mean length (mm) of colour morphs of ***Pomphorhynchus bulbocolli*** in white suckers. The top, middle, and bottom numbers represent mean length, number of worms meas[illegible] and standard deviation, respectively.

		Section of Intestine									
Sex of Worm	Colour of Worm	3	4	5	6	7	8	9	10	F	Prob
Male	Cream	8.8	9.1	9.5	9.4	9.7	10.1	10.0	8.6	3117.67	0.0000
		3	38	44	199	694	941	286	100		
		1.39	0.29	0.36	0.16	0.09	0.04	0.12	0.19		
	LY	12.1	11.8	12.2	12.1	11.8	11.4	11.2	9.2	1038.84	0.0000
		6	15	29	143	1000	532	19	6		
		0.74	0.52	0.34	0.19	0.07	0.10	0.55	0.43		
GF	Cream	11.6	11.9	12.8	12.7	12.3	12.1	12.7	11.9	523.89	0.0000
		6	10	22	148	542	900	215	63		
		0.69	0.46	0.51	0.16	0.22	0.06	0.12	0.21		

Table 22 continued:

Sex of Worm	Colour of Worm	Section of Intestine									
		3	4	5	6	7	8	9	10	F	Prob
GF	LY	16.1	13.7	14.4	13.8	13.5	13.5	12.9	12.5	757.64	0.0000
		1	14	44	217	1506	707	28	6		
		0.00	0.69	0.34	0.21	0.06	0.09	0.41	0.67		
NGF		9.2	8.4	8.1	8.2	8.2	8.3	9.0	8.8	891.22	0.0000
		5	28	48	135	359	340	170	83		
		0.37	0.23	0.25	0.13	0.07	0.10	0.14	0.19		

Table 22 continued:

Sex of Worm	Colour of Worm	Section of Intestine 3	4	5	6	7	8	9	10	F	Prob
Male	All	11.0	9.9	10.6	10.6	11.0	10.6	11.6	8.6	11835.12	0.0000
		9	53	75	345	1762	1499	265	106		
		0.82	0.30	0.29	0.14	0.06	0.05	0.09	0.18		
GF	All	12.6	13.1	13.9	13.4	13.3	12.2	12.7	12.0	16737.06	0.0000
		8	27	67	380	2246	1730	243	69		
		0.86	0.44	0.30	0.14	0.07	0.11	0.12	0.20		

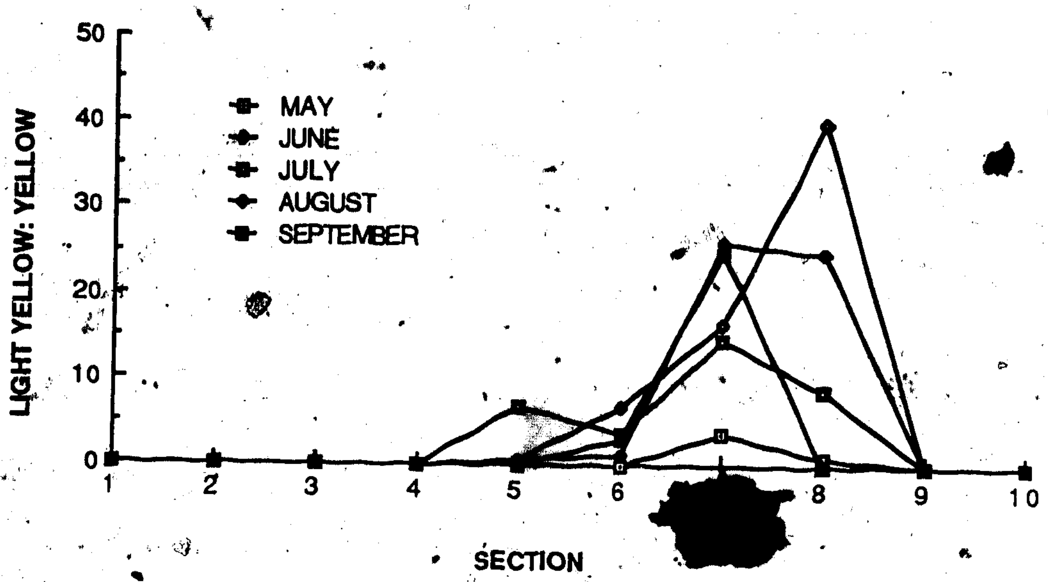


FIGURE 14: Light Yellow: Yellow ratios of *Pomphorhynchus bulbocolli* among sections of the intestine of white suckers in different months.

expected to be fertilised but were not, occurred in sections 9 and 10. The ratio of [illegible] to light yellow worms, which should be inversely related to development, was significantly higher in sections 9 and 10. And generally, male and gravid females in section 10 were significantly smaller in size than those in the other sections.

E. CROWDING

Stepwise regression analysis was used to determine the relationship between intensity of infection and host age, size and intestinal length in each sex of host; the results are shown in Table 23. The most important independent variable was host size ($r^2=0.42$, slope=0.12 worms (log units) per cm. increase in size of host, prob=0.0001 in male fish; $r^2=0.18$, slope=0.03 worms (log units) per cm. increase in size of host, prob=0.0276 in female fish). Once host length was factored out, the only other important variable was gut length (in male fish; r=0.65, slope=-0.02 worms (log units) per cm. increase in gut length, prob=0.0210). Age was not important in either sex. It is therefore concluded that increasing intensity is essentially a function of host size.

One common effect of crowding on helminth populations is that the range occupied is extended, but there is no change in the preferred location. That is, the first individual would be located more anteriorly and the last individual more posteriorly, but the location of the median individual would not change, with increasing intensity of infection. To test for these patterns, the four parameters of location in individual fish were regressed on intensity. The results (Table 24) were as expected. The location of the median worm did not change, whereas the location of the first worm moved significantly anteriad, that of the last worms moved significantly posteriad, and the range occupied was significantly extended, with increased intensity. The regression statistics (Table 24) indicate that these patterns are strong (the anterior and posterior positions are moved approximately 14 and 8% of the intestinal length with each log increase in intensity), and account for moderate proportions of [illegible]

Table 23: Stepwise regression analyses of intensity of infection with *Pomphorhynchus bulbocolli* on age (yrs), size (cm), and intestinal length (cm) of white suckers. ([illegible] (x+1)transformed intensity data from July sample only).

Female Fish					
Source	SS	DF	MS	F	Prob.
Reg.	0.4914	1	0.4914	5.5050	0.0276
Error	2.1425	24	0.0893		
Total	2.6339	25			
R=0.4320		R-Square=0.1866			SE=0.2988
Variable	Partial	Coeff	S.E	T-Stat	Prob
Constant		1.3467	0.4230	3.1837	0.0040
Size	0.4320	0.0320	0.0136	2.3463	0.0276
Remaining		Partial			Prob
Age		0.1215			0.5630
Int. L.		-0.0411			0.8453

Table 23 continued:

Male Fish

Source	SS	DF	MS	F	Prob.
Reg.	4.5867	2	2.2933	10.2260	0.0005
Error	6.2792	28	0.2243		
Total	10.8660	30			

R = 0.6497 R-Square = 0.4221 SE = 0.4736

Variable	Partial	Coeff	S.E	T-Stat	Prob
Constant		0.2491	0.7003	0.3558	0.7247
Size	0.6496	0.1174	0.0260	4.5215	0.0001
Int. L.	-0.4196	-0.0229	0.0094	-2.4459	0.0210

Remaining	Partial	Prob
Age	0.0761	0.6947

Table 24: Summary of regression analyses of four measures of the location of *Pomphorhynchus bulbocolli* on intensity of infection ($\log(x+1)$ transformed) in white suckers.

Location	DF	F	Prob	R^2	Coeff
Median	1, 178	0.1457	0.7031	0.0008	0.2997
Anterior	1, 178	39.0760	0.0000	0.1800	-13.5230
Posterior	1, 178	73.8500	0.0000	0.2944	8.3456
Range	1, 178	89.0470	0.0000	0.3347	21.8800

variance (approximately 18% of the variance in the anterior position, 29% in the posterior, and 33% in the range occupied).

It would be expected that any change with an increase in intensity would affect, primarily, the younger, more recently acquired worms (cream and light yellow) and not the older, dark yellow worms, which, presumably, arrived at the site first. When the locations of the various colour morphs were regressed on intensity, the results were as expected (Table 25). Yellow and dark yellow worms were not affected, nor were there significant changes in the location of the medianth cream or light yellow worms. However, the anterior position of cream and light yellow worms were moved anteriad, approximately 5% and 4%, respectively, of the gut length with each log increase in intensity, accounting for 17% and 8% of the variance. The posteriormost cream and light yellow worms were moved about 4% posteriad with each log increase in intensity, accounting for only 19% and 17% of the variance. The range also increased, accounting for 32% and 22% of the variance.

The range occupied may be extended under crowded conditions because new arrivals tend to establish more anteriorly or posteriorly, or both. To test this, the percentages of small, recently acquired worms (of the total number of small worms established in the fish) in sections 7 and 8 (combined) and 9 and 10 (combined) were regressed on total number of worms (log-transformed). The hypothesis is that with increasing intensity of infection, relatively more small worms would establish in the less populated, unpreferred sections 9 and 10, whilst there would be a negative relationship in the heavily populated, preferred sections 7 and 8. The results (Table 26) indicated no relationship in any month, with the exception of July, when the relationships were opposite to those expected.

To determine the effect of crowding on establishment / survival, the percentage (of the total number of worms in the fish) of small, recently acquired worms was regressed on intensity (log-transformed). The expectation, in this case, was that as the number of worms increased, the proportion of worms establishing would decrease. The results, presented in Table 27, indicated a significant decrease with increasing intensity in June, July, and August,

Table 25: Summary of regression analyses of four measures of the location of different colour morphs of *Pomphorhynchus bulbocolli* on intensity of infection (log (x + 1)-transformed) in white suckers.

Colour	DF	F	Prob	R^2	Coeff
			Median		
Cream	1, 172	1.1130	0.2929	0.0064	-0.0062
LY	1, 169	1.9114	0.1688	0.0112	0.0072
Yellow	1, 57	1.2537	0.2675	0.0215	0.0537
DY	1, 14	1.7560	0.2063	0.1115	0.7265
			Anterior		
Cream	1, 172	34.140	0.0000	0.1656	-0.0543
LY	1, 169	14.293	0.0002	0.0780	-0.0365
Yellow	1, 57	0.00003	0.9953	0.0000	-0.0005
DY	1, 14	0.4396	0.5181	0.0305	0.4137

Table 25 continued:

Posterior

Colour	DF	F	Prob	R^2	Coeff
Cream	1, 172	40.469	0.0000	0.1905	0.0390
LY	1, 169	35.025	0.0000	0.1717	0.0392
Yellow	1, 57	2.8208	0.0985	0.0472	0.1150
DY	1, 14	3.0908	0.1006	0.1809	1.0853

Range

Colour	DF	F	Prob	R^2	Coeff
Cream	1, 172	80.372	0.0000	0.3185	0.0932
LY	1, 169	47.947	0.0000	0.2210	0.0757
Yellow	1, 57	1.178	0.2823	0.0203	0.1155
DY	1, 14	1.465	0.2461	0.0948	0.6716

Table 26: Summary of regression analyses of the percentage of small (<6.0 mm) *Pomphorhynchus bulbocolli* (of the total number of small worms in the fish) in optimum and unsuitable habitats on intensity of infection (log (x+1)-transformed) in white suckers in different months.

Month	DF	Section	Coeff	Prob	R^2
June	1, 12	7+8	-0.75	0.1798	0.14
	1, 12	9+10	0.24	0.4037	0.06
July	1, 5	7+8	0.58	0.0082	0.78
	1, 5	9+10	-0.24	0.0082	0.78
August	1, 11	7+8	-0.45	0.3960	0.07
	1, 11	9+10	0.27	0.5943	0.03
Sept	1, 11	7+8	0.01	0.9882	0.00
	1, 11	9+10	-0.04	0.7871	0.01

Table 27: Summary of regression analyses of the percentage (arcsine-transformed) of small ($\leq$6.0 mm) *Pomphorhynchus bulbocolli* on intensity of infection (log (x+1)-transformed) in white suckers in different months.

Month	DF	Prob	R	R^2	Coeff
June	1, 12	0.0276	0.59	0.34	-0.03
July	1, 5	0.0065	0.89	0.80	-0.08
August	1, 11	0.0070	0.71	0.50	-0.03
Sept	1, 11	0.8644	0.05	0.003	0.007

but no relationship in September (possibly due to the relatively low numbers of worms encountered). The relationships were strong (3-8% decrease in percentage of small worms with a log increase in intensity) and important (accounting for 34-80% of the variance).

Crowding is known to result in poor survival or development; to test this, the survival / development indices (cream:light yellow, and light yellow:yellow ratios) were regressed on intensity (log-transformed). The results, presented in Table 28, indicate that crowding has no effect on survival or development to the next stage.

One other common effect of crowding is a reduction in size of worms. Two analyses were used to investigate this. First, the size of cream and light yellow worms (which occurred in large numbers in all months) were compared among months. In July, most categories of worms were significantly smaller than those in other months (Table 29). This was the month with the fewest small worms, the smallest proportion of non-gravid females, the most gravid females and the highest intensities. Second, the sizes of worms in the July sample were regressed against intensity (log-transformed). As can be seen in Table 30, with the exception of cream gravid females, there was no significant change in the size of the worms as intensity increased. The absence of a consistent correlation between worm size and intensity weakens (but does not eliminate) the case for an effect of crowding on worm growth (see Discussion).

To determine whether or not crowding has any effect on egg production, the percentage of gravid females was regressed on intensity (log-transformed). The hypothesis being tested is that as the number of worms increased, the proportion of gravid females would decrease. The results, presented in Table 31, showed that the expected negative correlation was obtained only in June; for other months, there was no correlation between egg production and intensity of infection.

An increase in maturation with increasing intensity could be due to increased copulation and, therefore, fertilisation. To test this hypothesis, the proportion of gravid females was regressed on the number of males (log-transformed). With the exception of July (which showed no correlation), an unexpected negative correlation was obtained in all other months (Table 32).

Table 28: Summary of regression analyses of the survival and development indices of *Pomphorhynchus bulbocolli* on intensity of infection (log(x+1)-transformed) in white suckers in different months.

Index	Month	DF	F	Prob	R²	Coeff
LY	June	1, 55	0.4877	0.4879	0.008	-2.24
	July	1, 53	0.5748	[illegible]	0.010	-2.91
LY:Y	June	1, 22	1.0956	[illegible]	0.047	[illegible]
	July	1, 22	0.2798	0.6021	0.013	[illegible]

Table 29: Mean length (mm) of cream and light yellow *Pomphorhynchus bulbocolli* in white suckers in different months.

Colour of Worm	Sex of Worm	Month	Number of Worms	Ave.L (mm)	SD
Cream	Male	June	890	9.50	0.05
		July	687	10.15	0.07
		August	285	10.00	0.14
		September	443	9.80	0.12
F	7674.56		Prob	0.0000	
LY	Male	June	344	12.29	0.11
		July	722	10.85	0.08
		August	331	12.09	0.12
		September	353	12.41	0.12
F	27216.70		Prob	0.0000	

Table 29 continued:

Cream	GF	June	544	12.26	0.08
		July	762	11.82	0.07
		August	288	12.76	0.11
		September	372	12.78	0.31
F	4518.72		Prob	0.0000	
LY	GF	June	612	14.01	0.09
		July	955	12.73	0.08
		August	517	13.65	0.10
		September	439	14.33	0.11
F	40562.59		Prob	0.0000	

Table 30: Summary of regression analyses of mean length of each colour morph of *Pomphorhynchus bulbocolli* on intensity of infection (log (x+1) transformed) in white suckers. (July sample only)

Section 7

Colour	Sex	DF	F	Prob	R	R^2	Coeff
Cream	Male	1, 18	2.9965	0.1005	0.3778	0.1427	-1.8382
	GF	1, 18	2.5732	0.1261	0.3537	0.1251	-1.3646
LY	Male	1, 18	0.6805	0.4202	0.1909	0.0364	2.2889
	GF	1, 19	1.8792	0.1864	0.3000	0.0900	-1.2202
Y	Male	1, 9	0.0002	0.9899	0.0043	0.00002	-0.0252
	GF	1, 15	0.0391	0.8459	0.0510	0.0026	0.2685

Section 8

Colour	Sex	DF	F	Prob	R	R^2	Coeff
Cream	Male	1, 22	0.1378	0.7141	0.0789	0.0062	-0.2348
	GF	1, 21	6.4549	0.0190	0.4849	0.2351	-1.0588
LY	Male	1, 20	0.0044	0.9480	0.0148	0.0002	-0.0574
	GF	1, 22	0.8962	0.3541	0.1979	0.0391	-0.5334
Y	Male	1, 4	0.6530	0.4644	0.3746	0.1403	1.6150
	GF	1, 8	3.1174	0.1155	0.5295	0.2804	-3.7811

Table 31: Summary of regression analyses of percentage (arcsine-transformed) of gravid female *Pomphorhynchus bulbocolli* on intensity of infection (log (x+1)-transformed) in white suckers in different months.

Month	DF	F	Prob	R^2	Coeff
June	1, 58	4.1112	0.0472	0.07	-0.09
July	1, 53	3.3894	0.0712	0.06	0.08
Aug	1, 48	1.1502	0.2889	0.02	-0.04
Sept	1, 40	2.6158	0.1137	0.06	-0.09

Table 32: Summary of regression analyses of the percentage (arcsine-transformed) of gravid female *Pomphorhynchus bulbocolli* on the numbers of male *P. bulbocolli* (log (x+1)-transformed) in white suckers in different months.

Month	DF	F	Prob	R^2	Coeff
June	1, 58	6.4881	0.0135	0.10	-0.11
July	1, 53	0.2599	0.6123	0.01	0.02
August	1, 48	5.2547	0.0263	0.10	-0.09
Sept	1, 40	9.8964	0.0031	0.20	-0.16

Crowding did not have any significant effect on embryonation. When the percentage (arcsine-transformed) of yellow and dark yellow worms (combined because of their small numbers) was regressed on intensity (log-transformed), the results showed no significant correlation in either June or July (the two months with the highest intensities and the highest numbers of yellow and dark yellow worms) (Table 33); this suggests that crowding has no significant effect on embryonation. However, regression of the number of yellow and dark yellow (combined and log-transformed) on intensity (log-transformed) gave a significant positive correlation with intensity (Table 33).

Table 33: Summary of regression analyses of the numbers (log (x + 1)-transformed) and percentage (arcsine-transformed) of yellow and dark yellow female *Pomphorhynchus bulbocolli* on intensity of infection (log (x + 1)-transformed) in white suckers in different months.

Month	DF	F	Prob	R^2	Coeff
			Log Numbers		
June	1, 58	10.4220	0.0021	0.152	0.33
July	1, 55	9.8650	0.0027	0.152	0.43
			Percent		
June	1,58	0.0065	0.9359	0.0001	0.0004
July	1,53	0.0504	0.8232	0.001	0.0063

I. DISCUSSION

In the introduction the confusion associated with the use of the terms "mature" and "gravid" females was pointed out, and a distinction made between mature, gravid, and ripe females acanthocephalans, based on their reproductive cycle. In this section, the subject is discussed further, along with some of its ecological implications.

In the present study, females *Pomphorhynchus bulbocolli* became sexually mature at 10 mm, when almost all became fertilised and were converted into gravid females; however, a few sexually mature but non-gravid females (with unshelled or unfertilised eggs) larger than 10mm were found. The paucity of such females suggests that the processes of mate-finding and fertilisation are efficient; their presence may indicate a breakdown in one of these processes. Only if a clear distinction is made between sexually mature and gravid worms can the effectiveness of these processes be evaluated. Sexually mature females are, therefore, not necessarily gravid and a clear distinction should be made between sexual maturation and egg production.

Similarly, gravid female acanthocephalans do not all have eggs at the same stage of embryonation. For example, in this study, four colour morphs of gravid females were found. The lightest-coloured females were the smallest and their eggs were in early stages of embryonation, whilst the darkest females were the largest and were the only ones which carried ripe and infective acanthors. The presence of "gravid" females has often been interpreted as indicating that infective eggs could be (or are being) shed at the same time (or from that host species) (for examples, see Holmes *et al.*, 1977; Muzzall, 1980; Gleason, 1984; and Walkey, 1967). Such interpretations could be grossly in error if (as in this study) only a small proportion of females are actually carrying fully embryonated eggs, or if ripe females are limited to a restricted group of host species. A similar error may be the underlying cause of some unsuccessful attempts at establishing infections in the laboratory. It is, therefore, important that a clear distinction be made between gravid (egg-producing or egg-bearing) and ripe (egg-releasing) females.

Awachie (1966) recognised four colour morphs of *Echinorhynchus truttae* and demonstrated that the colour morphs differed in size and stage of sexual maturity of female worms. He concluded that colour may serve as a rough guide to the age and stage of maturation of worms. In this study, a similar relationship between colour, size and stage of embryonation was found in *Pomphorhynchus bulbocolli*. Many other adult acanthocephalan species, for example *Polymorphus minutus*, are also coloured. In such species, colour may be a useful indicator of age or maturation. Van Cleave & Rausch (1950) suggested that the colour might be due to carotenoids, and Barrett and Butterworth (1968) identified the pigment in the cystacanth and adult *Polymorphus minutus* as a carotenoid, esterified astaxanthin. The function of carotenoids in acanthocephalans is not known. In an attempt to establish their role in adult *P. minutus*, Barrett and Butterworth (1968) fed laboratory-infected ducks carotenoid-deficient diets. Adult *P. minutus* recovered from the ducks were nearly colourless and yet appeared normal in size and produced viable eggs, suggesting that the pigment has no necessary relationship with either growth of the worms or the maturation of eggs. It seems, therefore, that the pigment is obtained from the diet and is absorbed in minute quantities during the life span of the parasites so that older parasites are more intensely coloured.

The present level of understanding of the factors which control the dynamics of parasitic helminth populations has been enhanced by the development of mathematical models by researchers like Anderson and May (1979) and May and Anderson (1979). However, as noted by Anderson (1976), one of the main difficulties in these models is that quantitative studies of the rate parameters which control the flow of organisms through a parasitic life cycle have been made in only a few cases. Holmes *et al.* (1977), for example, derived relative flow rates for *Echinorhynchus salmonis* in a community of fishes in Cold Lake, Alberta, and concluded that most of the flow of *E. salmonis* in the system was through whitefish, based on the relative numbers of gravid females of each host species. It was assumed that all gravid females in all the host species produced the same number of eggs, and that those eggs were infective or were at the same stage of embryonation. Gravid female *E. salmonis* in white suckers collected from Muriel Lake, Alberta, differed in intensity of colour (personal observation), suggesting that their eggs might be in different stages of development. In the present study, ripe female *P. bulbocolli* formed only a small proportion of female worms, suggesting that at any one time only a small proportion of the females were actually releasing infective eggs (or that ripe females have a very short life-span and drop out or die shortly after egg-release). If this proportion differed amongst host species, the relative numbers of ripe females could have been very different than the relative numbers of gravid females amongst host species. Thus, the use of ripe, instead of gravid, females in the *E. salmonis*-fish model could make major differences in the flow rates derived. The same argument suggests that caution should be used in making predictions about the population dynamics of parasitic helminths based on gravid rather than ripe females.

A. SEASONAL PATTERNS

In the introduction it was shown that the biology of a given species of acanthocephalan may vary from one geographic location to the next, whether in the same or different host species. This has been recognised by Chubb (1982) and reported in a number of parasite species, including *Pomphorhynchus bulbocolli*. Amin (1987a) found in a number of host species (including *Cyprinus carpio* and *Catostomus commersoni*) that prevalence and intensity of infection with *Pomphorhynchus bulbocolli* increased from low in the autumn (late October through November) to maximum in the summer months (June through July and early August); recruitment occurred throughout the year. In *Cyprinus carpio* both prevalence and intensity of infection were low in autumn, decreased in winter, increased in spring, and reached a high in summer; recruitment was high in autumn, decreased in winter, peaked in spring, and decreased in summer (Amin, 1987a). In *Catostomus commersoni*, prevalence was highest in autumn and decreased to about the same level in spring and summer, and intensity of infection was highest in autumn and very low in spring and summer; recruitment occurred mainly in spring (Amin, 1987a).

Seasonal cycles have also been reported for some other *P. bulbocolli*-fish systems. Lawrence (1970) reported that in *C. commersoni* from Maine, U.S.A., prevalence was high throughout the year but intensity was low in fall and winter, increasing to a peak in summer. For *Hypentelium nigricans* from Kentucky, Gleason (1984) reported that prevalence was highest in autumn (October through December) and decreased to a low in winter (January through March), whilst intensity of infection was low in autumn, decreased in winter, and increased through spring (April through June) to a maximum in summer (July through September); recruitment did not occur in winter because no immature females (with ovaries intact) were found then. Prevalence and intensity of infection of *Leuciscus cephalus albus* from Yugoslavia with *P. bosniacus* peaked in summer (August) (Kazic, 1970).

In the present study, prevalence of infection of *C. commersoni* with *P. bulbocolli* was 100% in all months but intensity of infection was high in spring, increased to a maximum in early summer (July), and decreased in late summer; recruitment occurred throughout the year. This pattern is similar to that reported for the other *P. bulbocolli*-fish systems mentioned above, with the exception of that reported for for *C. commersoni* by Amin (1987a). Amin (1987a) indicated that the autumn peak in *C. commersoni* may have been due to the presence of a large number of female fish (75%) in the sample, but this is not satisfactory; another factor may be responsible for this.

The seasonal pattern of intensity of infection of white suckers with *P. bulbocolli* observed in the present study is undoubtedly due to a shifting balance between recruitment and loss of worms. Infective larvae were available all year round so intensity of infection increased from May to July probably due to increased feeding by the white suckers as water temperatures rose, and decreased due to reduced feeding at the lower water temperatures of August and September.

Amin (1987a) indicated that the type of seasonality where greatest egg production, prevalence and intensity of infection occurs in summer, and greatest recruitment occurs in autumn and summer could be related to extreme seasonal temperature variations which usually involve freezing-over during the winter. For example, in southeastern Wisconsin, *Acanthocephalus dirus* from Pike River, which freezes over in the winter, showed peak prevalence, intensity, and egg production in spring in both creek chub and white sucker

(Amin, 1975b), whilst *Echinorhynchus salmonis*, from Lake Michigan, which does not freeze over, showed no seasonal pattern (Amin and Burrows, 1977). Both Tichigan Lake (Amin, 1987a) and Tyrrell Lake (the site of the present study) freeze over in winter and the fact that *C. commersoni* showed a different pattern from the other fishes studied by Amin (1987a) and the present study suggests that freeze over is not the only factor in play. The variations in the details of the seasonal cycle, therefore, suggest the interaction of various factors, some of which are temperature, host feeding activity, availability of infective larvae, migration of the intermediate or definitive host, composition of the vertebrate community, and the type of water body.

It would be expected that the proportion of small, recently acquired worms would be higher in July, when feeding was more intense. Recruitment appeared to occur throughout the year presumably due to availability of infective larvae (although data from the winter period are scarce) but there was, however, a midsummer low. Three factors, acting independently or in an interactive manner, could have caused the low level of recruitment in July. These are 1) a change in the food habits of the fish, 2) temperature-dependent rejection response described by Kennedy and Walker (1969), and 3) faster growth of the newly established worms at the higher temperatures of July.

In July, as opposed th the other months, white suckers consumed relatively more food items (algae, molluscs, *etc.*) other than amphipods. Data were not adequate to assess whether they consumed less, the same, or even larger quantities of the intermediate host. The fact that recruitment was low suggests that they may have eaten less, but some other factor(s) may be in operation too.

The temperature-dependent host response put forward and demonstrated by Kennedy and Walker (1969) and Kennedy (1971) could have been responsible for the pattern of recruitment observed in the present study. The proportion of newly established worms decreased between May and July, when temperatures were rising, and increased in August and September, when temperatures were dropping, a pattern consistent with a temperature-dependent resistance.

The apparent stimulatory effect of temperature on growth and development of acanthocephalans in the field has been reported by various workers. Hine and Kennedy (1974b), for example, reported that in graylings mature (no gravid females were found) *Pomphorhynchus laevis* occurred throughout the year but were more common between May and July. They further reported that in the intermediate host, *Gammarus pulex*, later stages of larval *P. laevis* occurred in greater proportions in summer. The proportion of acanthellae in the earlier stages of development increased as temperatures fell, reaching highest values in winter, and decreased as temperatures rose, reaching low values in summer. Awachie (1966) demonstrated in experimental infections, at various temperatures, that growth and development of *Echinorhynchus truttae* in *Gammarus pulex* was retarded at low temperatures. In one experiment conducted at 2-4°C, only spherical and earlier stages were recovered after 136 days; these stages were normally recovered after 20-24 hours at room temperature. Similarly, growth and development of *E. truttae* in the definitive host, *Salmo trutta*, were inhibited at low temperatures (Awachie, 1966). This apparent effect of temperature on growth and development, combined with Amin's (1987b) observation that growth of *Pomphorhynchus bulbocolli* was most rapid in worms less than 6 mm in length could, in addition, explain the low proportions of recently acquired worms (up to 6 mm in length) and non-gravid female *P. bulbocolli* encountered in July in the present study.

Another factor, in addition to reduction in feeding activity, which may have contributed to the decline in intensity of infection in late summer is the loss of worms. Two types of losses may be distinguished, prereproductive (cream, light yellow, and yellow worms, probably due to maximal effects of crowding in July, as demonstrated by Brown (1986)) and postreproductive (dark yellow worms). The survival indices (cream:light yellow, light yellow:yellow) indicate loss of worms between July and August when the intensity of infection dropped sharply. There was a slight increase in the cream:light yellow ratio, and a sharp increase in the light yellow:yellow ratio during this period, suggesting a strong pre-reproductive loss.

Pomphorhynchus bulbocolli showed a limited seasonal cycle of egg production (i.e., variation in the occurrence of gravid females) in the present study, both the percentage and numbers of gravid females reaching high levels in early summer, and coinciding with the period of high water temperatures. A similar pattern has been reported for *Pomphorhynchus bulbocolli* by Amin (1987a).

One other feature of the biology of acanthocephalans which may exhibit a seasonal pattern is egg release (by ripe females). For example, Brattey (1988) reported a seasonal cycle of egg release by *Acanthocephalus lucii* in perch, egg production reaching a peak in spring and summer, and egg release probably occurring in summer and fall. This may be difficult to detect, especially in situations where gravid females and ripe females are not distinguished. For example, Gleason (1984) reported that gravid female *P. bulbocolli* occurred all year round and implied that egg release occurred all year round. However, after finding that recruitment in the amphipod intermediate host was seasonal, Gleason (1987) suggested that egg release by *P. bulbocolli* may be seasonal. In the present study, ripe females were restricted to early summer, suggesting that egg release was seasonal.

There are, apparently, two types of egg release by acanthocephalans, species in which worms (including ripe females) are shed whole (e.g., *Acanthocephalus jacksoni* - Muzzall and Rabalais, 1975b) and those in which shelled acanthors are discharged into the intestinal lumen of the definitive host to be, eventually, passed out with the faeces (e.g., *Polymorphus minutus* - Whitfield, 1970). In the present study, the disappearance of ripe females coincided with a sharp drop in intensity of infection, suggesting that *Pomphorhynchus bulbocolli* belongs to the first group and does not release shelled acanthors into the intestinal lumen of the fish host.

Many studies have indicated that in acanthocephalan infections the sex ratio varies from close to unity in new infections to one significantly in favour of females in old infections (Awachie, 1966; Crompton and Whitfield, 1968; Amin and Burrows, 1977; Amin, 1987a; and others). This phenomenon has been demonstrated in laboratory infections by Awachie (1966) who found that male *Echinorhynchus truttae* began to drop out of the intestine of brown trout by 45 days and none remained after 82 days postinfection; females were first found in the faeces 69 days postinfection and none was present at the end of 14 weeks (Awachie, 1963). In the present study, the male to female ratio also became progressively smaller with increasing colour intensity. These variations in sex ratio with age suggest that males die earlier than females.

The generally held view is that females occur in relatively larger numbers than males in old acanthocephalan infections because males die after copulation. If this were so, it would be expected that the ratio would change in favour of females with season, the ratio being close to unity at the time of recruitment and in favour of females at the time of sexual maturation and egg production. Amin and Burrows (1977) reported such a pattern in *Echinorhynchus salmonis*, the sex ratio being close to even in winter (time of recruitment) and shifting in favour of females during spring and early summer (time of sexual maturation and egg production). In contrast, Gleason's (1984), Amin's (1987a) and the present study indicate that the sex ratio of *Pomphorhynchus bulbocolli* does not change significantly with season, casting doubt on the suggestion that males die after copulation. Kennedy (1972b) demonstrated, in experimental infections, that female *P. laevis* were relatively more abundant than males during the first two weeks of the infection but, thereafter, the ratio was in favour of males. It appears, therefore, that some other factor(s) rather than death of males after copulation is involved. One possibility is that females absorb carotenoids at a faster rate, therefore develop a deeper colour despite being the same age.

The influence of temperature, considered the most important environmental factor controlling the seasonal cycles of parasitic helminths, has been discussed by Chubb (1982). Its role, as it relates to recruitment, intensity of infection, and growth and development, has been mentioned above. Other aspects of the biology of parasitic helminths which have been reported to be influenced by temperature are egg-production and embryonation.

There are conflicting reports in the literature about the effects of temperature on egg production and embryonation in parasitic helminths. Data obtained from laboratory experiments by Brattey (1982) support the hypothesis that embryonation is controlled by temperature. He demonstrated that *Acanthocephalus lucii* infections in perch kept at 19 and

12°C developed shelled acanthors in about 3 and 7 weeks, respectively. At 5°C, however, embryonation was almost completely inhibited so that shelled acanthors were not completely developed after 13 weeks. In the present study, the restriction of ripe females to the time of rising water temperatures also suggests that temperature is crucial for embryonation. Although temperature does not seem to be a critical factor in the production of shelled eggs (gravid females were found in other months, including winter), high temperatures do seem to accelerate the process, as evidenced by the relatively high proportions of gravid females in July. This lends support to Kennedy's (1975) warning that the correlation between temperature and sexual maturation / egg production should be applied with caution since in some systems other factors seem to be more important.

The relationship between hormone levels of the female host and sexual maturation / egg production of helminth parasites have been documented by several workers, including Kennedy (1969, 1975), Wootten (1974), and Amin (1975b, 1978); in all such cases sexually mature or spawning females tend to have relatively more gravid worms. No such evidence was found in this study, gravid females of all the colour morphs occurring in both sexually immature and mature female white suckers. Host hormone levels, therefore, are not important in egg production and embryonation in this system.

So far, it has been concluded, from this study, that intensity of infection, egg production, and egg release show seasonal patterns, often correlated with temperature. But what role does temperature actually play in determining these patterns? It has been implicated in all the patterns seen in this study, but to answer the question precisely will require laboratory experiments. The difficulty associated with establishing laboratory infections, unfortunately, made such a study impossible.

B. HABITAT SPECIFICITY

Pomphorhynchus bulbocolli, like most parasitic helminths, exhibits habitat specificity, all age and sex categories being concentrated in the 60-80% region of the intestine, irrespective of season. Amin (1987b) pointed out that there is no migration of *P. bulbocolli* from an area of settlement to an area of maturation. He reported that the small size of [illegible] proboscis hooks, and neck in recently acquired juveniles enable them to detach, mov[illegible], and reattach. Within 2-3 weeks after ingestion, however, there is a considerable increase in the size of these structures such that, once attached, worms 6 mm or more in length cannot detach and reattach, i.e., they are incapable of migration and live the rest of their lives wherever they initially established. Muzzall (1980) obtained similar results in white suckers, *P. bulbocolli* being concentrated in the 60-80% region of the intestine, with no evidence of migration. Similarly, no evidence of migration was found in the present study; there was no difference in attachment sites between males and females, no difference in sex ratio between sites, and only minor differences between young and old worms. *Pomphorhynchus bulbocolli* obviously falls into Crompton's (1973) group 1, parasites which arrive directly at their final site.

Small worms and non-gravid females constituted relatively higher proportions of the total numbers of worms in the unpreferred sites, whilst gravid females constituted relatively higher proportions in the preferred sites. These patterns would suggest that either establishment was lower in the already heavily populated preferred sites, or that growth, mating, or long-term survival was lower in the unpreferred sites. However, the actual numbers of worms establishing was highest in the preferred sites, eliminating the first possibility.

In natural infections, it is impossible to determine the age of the worms and, therefore, their growth rates. However, in such infections, the size attained may differ between optimum and unsuitable habitats. In natural infections of *Pomphorhynchus laevis* in grayling, chub, and barbel, Kennedy *et al.* (1976) recorded the greatest mean and maximum lengths in the preferred sites, with both measures declining anteriorly and posteriorly. Kennedy *et al.* (1976) suggested that unsuitable physico-chemical or feeding conditions were responsible for this. In the present study, worms of the same colour class were approximately the same size in all sections (except section 10 where they were smaller). However, because the range of the larger yellow and dark yellow worms was more restricted to the preferred

60-80% regions, these regions did have the largest worms, but mean length still did not differ among sections. Growth rates could be greater in these regions, but that could be detected only in experimental infections.

Differences in egg production among sites could be due to reduced chances of mating in the unpreferred sites. In the present study, large, sexually mature females, which would be expected to be fertilised, but were not, were found primarily in the unpreferred sites, and almost entirely in sections with few worms. Although males of average size were almost always present in the same (or adjacent) sections, distances separating male and female worms in these low density conditions could have prevented copulation. Unfortunately, specific locations of individual worms were not recorded, so this possibility cannot be tested. In any case, there were few large, unmated females, suggesting that problems with mating are not common.

There is more evidence for reduced survival in the non-preferred sites. The constancy of the cream:light yellow ratio between sections 3 and 8 suggests that the worms can establish, survive and develop equally well to the light yellow stage in these regions of the intestine. The significantly greater ratios in sections 9 and 10, plus the absence of yellow and dark yellow worms in these sections, suggest that worms do not live long enough in this region to attain egg-releasing age. In addition, comparison of the light yellow:yellow ratio indicates that survival and development to the yellow stage is not the same in all the anterior sections; the ratio is high in sections 7 and 8, the preferred sites, decreasing anteriorly. This pattern suggests that survival is poorer in the preferred sections, a suggestion that does not completely agree with other data. Perhaps, survival is actually better in the preferred sites but density-dependent constraints make development into the later stages more difficult in these sites (See Crowding for further discussion).

Complete development, therefore, depends on the site occupied. Although it may be difficult to do (especially where large numbers of parasites are involved), comparison of the developmental stages of female worms between sections may reveal similar differences in fitness between sections in some systems which have been reported to show no such differences. For example, Kennedy *et al.* (1976) did not recognise the various stages of maturation of eggs but concluded that *Pomphorhynchus laevis* is able to reproduce outside of its preferred zone because females containing shelled eggs were found in all the regions of the alimentary tract in which the parasite is found.

The unsuitability of the 80-100% region may be due to the physico-chemical and feeding conditions present there. As discussed above, almost all the worms in that section are cream in colour, and the evidence indicates that they do not live to egg-releasing age there. Figure 2 reveals that the 80-100% region is the posteriormost portion of the alimentary tract. In most organisms, relatively few digested products reach there, and relatively little absorption takes place there.

In conclusion, fitness of *Pomphorhynchus bulbocolli* depends on the site occupied. Larger worms and relatively more egg-producing and egg-releasing females are found in the 60-80% region than in the other regions, in spite of the large numbers of worms encountered in these optimum sites. The 30-60% region is a potentially suitable site but, apparently, survival to the later stages, yellow and dark yellow, is poor, whilst worms in the 80-100% region have difficulty surviving or developing to the light yellow stage. The 60-80% region is, therefore, the best site, followed by the 30-60% region; the 80-100% region is the worst site.

C. CROWDING

It would be expected that the restriction of *Pomphorhynchus bulbocolli* to the preferred sites in the intestines of white suckers, and the large numbers of worms encountered in the present study would initiate some density-dependent processes which would result in a decrease in fitness as intensity of infection increases. The results obtained were, however, not overwhelmingly conclusive.

There was no conclusive evidence for acceptance or rejection of the density-dependent process described by Brown (1986), but there was evidence for site extension. Evidence obtained for reduction of establishment, survival, and growth were contradictory, and there was no evidence for either a negative or positive effect on egg production. The only conclusive evidence obtained was, therefore, on site extension.

In the present study, a positive correlation was found between intensity and length of white sucker, and (in male fish) a negative one between intensity and deviations from the average gut length (i.e. when fish length was kept constant). Neither of these two results prove the presence or absence of a density-dependent process which determines the number of worms which an individual can sustain, and neither does it discount the alternative hypothesis that larger and older fish have more worms simply because they consume more food. The negative correlation between intensity of infection and the deviations from the average gut length may be attributable to the feeding habits of the fish and the conditions in its gut. In many species, the length of the gut is a function of the digestability of the diet. Whitesuckers feed on a variety of items, including amphipods (high digestability) and algae (low digestability). Thus, fishes with gut lengths above average may be feeding more on non-infective food, than on amphipods, thus reducing exposure to infective cystacanths. Thus, it appears that the feeding habits of the host are important and should be considered along with the age or size of the host.

The range occupied by the worms extended both anteriorly and posteriorly as intensity increased. However, only the range of cream and light yellow worms were extended, suggesting that these relatively young worms were forced to establish in the unpreferred sites. The reason for this is not clear.

Brown (1986) demonstrated a density-dependent establishment and survival of *Pomphorhynchus laevis* in laboratory-infected rainbow trout. A similar phenomenon may be operating in the present study, the proportion of small, recently acquired worms decreasing as intensity increased, but whether this was due to a direct decrease in the proportion establishing or death was not clear. The development or survival indices showed no significant relation with intensity, suggesting that the decrease in the proportion of small worms is probably due to a reduction in establishment, not death.

It was indicated that the light yellow:yellow ratio was higher in the preferred, heavily populated sites, suggesting poor survival or development to the next stage in these sites.

Evidence gathered from *Pomphorhynchus bulbocolli* infections in white suckers from Muriel Lake, Alberta (unpublished), and shown in Figure 15, indicates that survival is actually higher in the preferred sites; this suggests that the higher ratios in the preferred sites are probably due to reduced development to the yellow stage. This evidence, in addition to the fact that dark worms are restricted to the preferred sites and that their numbers increase with intensity, suggests that worms survive better in the preferred sites but under crowded conditions their development may be slowed down. Laboratory experiments involving primary and secondary infections carried out over a period of time will be needed to clarify the influence of crowding on establishment, survival, and development to the next stage.

The significant seasonal pattern of intensity resulted in significant differences in the size of worms among months in the present study. July had the smallest sizes of worms and the highest intensities, despite the relatively low intake and the highest temperatures which should result in faster growth. Regression analyses, however, failed to reveal any such relationship probably because of the mixed ages of worms dealt with, emphasising the need for laboratory experiments.

Increasing intensities may have one of two effects on egg production in acanthocephalan populations, a negative effect which results in a decrease, and a positive effect which results in an an increase in the percentage of gravid females. Two processes may be associated with the positive effect; 1) a density-dependent chemical stimulation of reproduction such that worms become reproductively active at an earlier age in the presence of other conspecifics, or 2) as intensities of infection increase the problem of pairing is resolved so that the proportion of fertilised females also increase. To test the first hypothesis and the negative effect, the percentage (arcsine-transformed) of gravid females was regressed on intensity (log-transformed); no significant relationships were obtained, suggesting the absence of both the negative and the positive effect. For the second hypothesis, the percentage (arcsine-transformed) of gravid females was regressed on the number of males (log-transformed); the results showed an unexpected significant negative correlation.

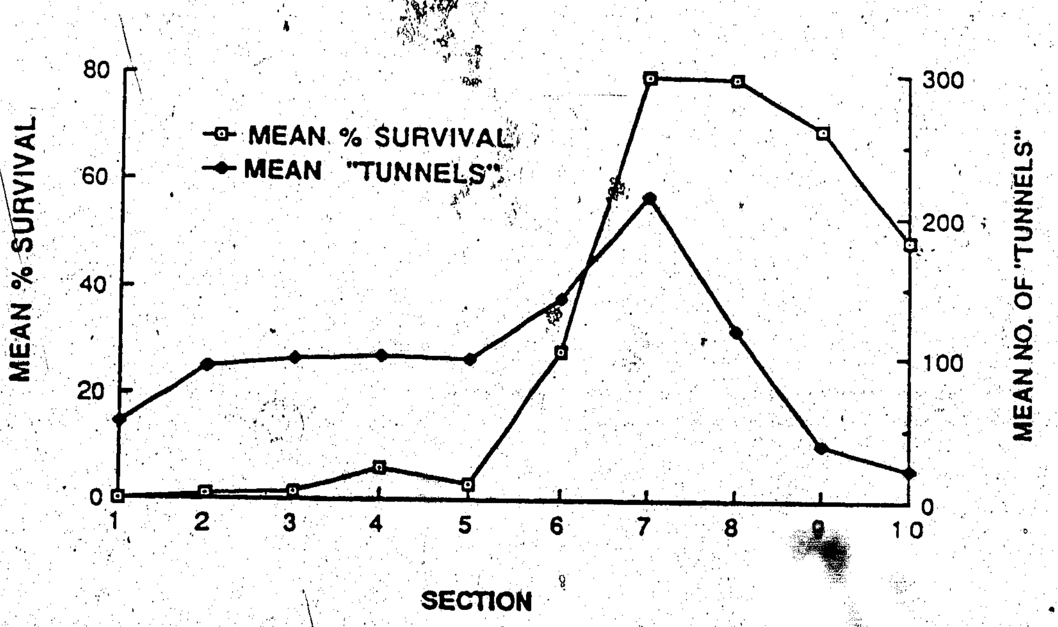


FIGURE 15: Mean number of "tunnels" and percent survival of *Pomphorhynchus bulbocolli* in the intestines of whitesuckers from Muriel Lake, Alberta. The "tunnels" are the connective tissue capsules formed by the penetration of the intestinal wall by the proboscis and neck and seen on the serosa. Calculation of percent survival (number of worms present in section x 100/ number of "tunnels" in section) was based on the assumption that each worm formed a "tunnel"; the disadvantage here is that sometimes, especially in sections 7 and 8, the number of worms is greater than the number of "tunnels", in which cases % survival was taken to be 100.

Some population models (for example, Macdonald, 1965) often have a lower unstable equilibrium point, termed the breakpoint, below which pairing cannot take place and the population runs to extinction; above this point, the probability of pairing increases with increasing density. The result is an increase in the proportion of fertilised females (positive effect) until an optimum density is reached, beyond which any further increase causes a decline in the proportion of gravid females (negative effect), probably because under the stressful conditions of overcrowding energy resources are diverted to survival instead of reproduction (Strecker and Emlen, 1953). The absence of any correlation between the percentage of gravid females and the intensity of infection suggests that there may be no density-dependent regulation or stimulation of egg reproduction in this system. In addition, the lack of a correlation between the percentage of gravid females and the number of males suggests that in this *Pomphorhynchus bulbocolli*-white sucker system intensities are such that pairing is not a problem, even though the probability of pairing may be low in unpreferred sites. The overall densities encountered would, therefore, tend to ensure transmission and perpetuation of the species.

Evidence has been provided to show that survival is better in the preferred, heavily populated sites and that crowding does not significantly influence survival, but it may slow down development. The results on growth (size) were conflicting, probably because of the different ages of worms involved, and a negative effect on egg production could not be shown. The inconclusive results demontrates the difficulty associated with determining the effects of crowding from field data, and the need for laboratory experiments to give some insight into field situations.

D. CONCLUSION

A clear distinction has been made between gravid and ripe female *Pomphorhynchus bulbocolli* in the present study, and evidence gathered indicate that 1) only dark yellow females carry ripe, infective eggs, 2) ripe females are restricted to the summer period, 3) complete development depends on the site occupied, and 4) that crowding appears to have some influence on the development of *P. bulbocolli*. Thus, some of the problems which prompted this study have become a bit clearer. A lot of field and experimental work is, however, still needed for a better understanding of the interaction between *Pomphorhynchus bulbocolli* and its hosts.

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