

The ecology of tapeworm parasites in wildfowl

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Introduction

The Anatidae, like most groups of vertebrates associated with freshwater or marine environments, are likely to be infected with a wide range of metazoan parasites. Of these, the tapeworms (Cestoda) are amongst the most abundant and ubiquitous. In a search of the literature, Lapage (1961) recorded more than 100 species of these worms. Many of these species may be synonyms, but nevertheless the total number must be very large. Individual birds may be heavily infected—burdens of 20-30 worms were found quite commonly in wild Mallard *Anas platyrhynchos* at Slimbridge, Gloucestershire (Avery 1966b), and Mallard and Canvasbacks *Aythya vallisneria* have been recorded as carrying exceptional infections of 15,000 and 40,000 worms respectively (Avery 1966b, Cornwell and Cowan 1963).

The purpose of this paper is twofold: to review advances in knowledge of the ecology of tapeworms in wildfowl since Lapage's paper, and to describe some experiments which were carried out at the Wildfowl Trust, Slimbridge, on the ecology of some of the commoner tapeworms of ducks. No attempt has been made to include work on the parasites of domestic ducks and geese, except where this is relevant to the ecology of wild birds, or to the problems of keeping wild birds in captivity.

Review of the literature

United Kingdom

Miscellaneous records of tapeworms from Anatidae have appeared in the literature for many years. Menzies and Venn (1952) and Venn (1953) recorded species which they considered to have caused the deaths of wildfowl at Slimbridge. Soulsby (1958) gave a more detailed list. This work was extended by Avery (1966a,b) who listed tapeworms and other parasites found in 123 Slimbridge birds which died in 1960 and 1961, and in 30 wild Mallard caught in the decoy. The most comprehensive account is that of Beverley-Burton (1964), who examined nine species of ducks from Nacton Decoy, Suffolk, St. James' Park, London, and Silwood Park, Buckinghamshire, and recorded and described 25 species of tapeworm parasites.

Europe and Asia

There have been no comparable attempts to list the tapeworms of wild

Anatidae in Western Europe. In eastern Europe and the U.S.S.R., however, there has been a considerable amount of work on the parasites of animals of economic importance, and more than 40 papers a year have recently been published on the parasites of ducks and geese. Most of these are surveys of the incidence of infection in domestic birds, or of methods of control of infection by pharmacological or husbandry techniques. They also include surveys of infection in wild birds carried out with the primary aim of determining whether the worms carried by these birds represent a potential threat to domestic poultry: for example Sultanov (1958), Kotelnikov (1962, 1963, 1964), Parukhin and Truskova (1963) and Dansan (1964). Recent papers on the infection of wild Anatidae with tapeworms include those of Macko (1961), Zajicek and Pav (1963) and Rysavy (1966) for Czechoslovakia; Korpaczewska (1963) for Poland; Sultanov (1963) for Uzbekistan; Maksimova (1963) for Kazakhstan; Gerasimova (1964) for Omsk; Khuan (1962), Oshmarin (1963) and Rizhikov (1963) for the far east of Siberia; and Tsimbalyuk (1965) for Komandorskye Island. Handbooks on parasites of domestic Anatidae and their control have been written by Czaplinski (1960b) and Rizhikov (1967), and there is a chapter by Shevtsov (1966) in I. N. Gladenko's book on farm stock and poultry.

North America

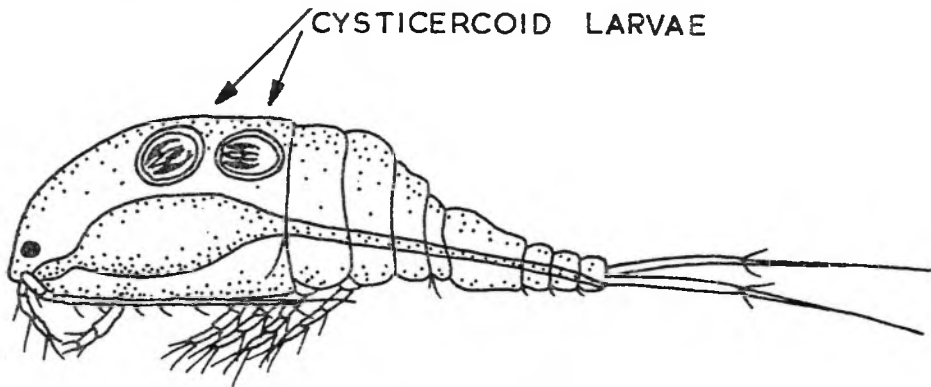
Recent studies on the helminth parasite fauna of North American Anatidae include those of Hanson and Gilford (1961), Buscher (1965, 1966) and Threlfall (1968). A particularly valuable contribution has been made by Cornwell and Cowan (1963). These authors examined 180 Canvasbacks and made a careful study of differences in the parasite fauna of birds of various ages and from several localities. They correlated the differences with changes in the feeding habits of the hosts. Ducklings were more heavily infected than adult birds, although worm burdens varied considerably, even between ducklings in the same brood. The adult ducks tended to lose their parasites during the summer moult, when they were feeding mainly on vegetable material.

Life cycles of the parasites

The life cycles of most of the commoner tapeworms found in wildfowl are well

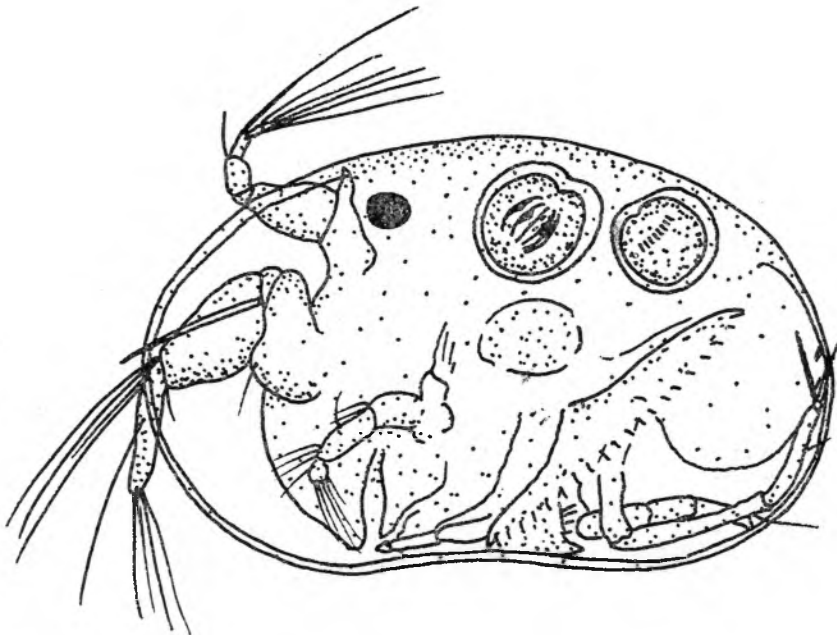
known. They involve a larval stage, called a cysticercoid, which is parasitic in the haemocoel of crustacea such as copepods and ostracods, and more rarely in cladocerans, and also in leeches or molluscs. A

specimen of the copepod *Cyclops strenuus* harbouring two cysticercoids of the tapeworm *Sobolevicanthus gracilis*, is shown in Figure 1, as is an infected ostracod.



0.5 MM

Figure 1. (A) A specimen of the copepod *Cyclops strenuus* infected with two cysticercoid larvae of the tapeworm *Sobolevicanthus gracilis*.



0.2 MM.

(B) An ostracod infected with cysticercoid larvae.

Polish workers have in recent years added to our knowledge of these life cycles, as part of an ecological survey of parasitism in the Mazurian Lakes (Rybicka 1958; Jarecka 1958, 1960, 1961; Rysavy 1961). The time which these larvae take to become infective depends on the temperature, but is usually two to three weeks (Petrochenko and Kotelnikov 1959; Czaplinski 1960a; Rysavy 1960 and others).

At Slimbridge, larval cestodes have been found in the copepod *Cyclops strenuus* and in the ostracods *Cyprina ophthalmica* and *Cypridopsis vidua*, all of which are abundant in the ponds. The species whose larvae have been found in these hosts are shown in Table I. No larvae were found in water fleas (cladocera) or in the water louse *Asellus*, which also occur in the ponds.

The biology of the parasites

General

Much of the work on tapeworms in Anatidae is descriptive, limited to listing the parasites, giving their numbers, or discussing their pathological effects. Little is known about the biology of the worms: it is not known how long they live, how many eggs they produce, or what their nutritional requirements are.

A number of experiments carried out at Slimbridge were designed to investigate some of these problems, in particular: 1) the growth rates and longevity of tapeworms in ducks infected under laboratory conditions; and 2) the ways in which tapeworm populations would develop in flocks of Mallard exposed to natural infection for extended periods of time.

Growth rates and longevity of tapeworms

Khaki Campbell ducklings were reared in the laboratory on bitumen-floored pens where they had no opportunity to acquire tapeworm infections, and at 27-34 days of age were fed 20 cysticeroid larvae by gelatin capsule (Parke Davis no. 5). Four birds were killed every three days and their tapeworms measured and weighed.

Two such experiments were performed: in Experiment 1 the birds were fed larvae of *Dicranotaenia coronula*, and in Experiment 2 those of *Sobolevicanthus gracilis*. These two species were chosen because they have larvae which are easily recognised under the low power of the microscope—the former species has a ring of several dozen small (20-30 microns) hooks on the rostellum, while the latter have only eight hooks which are comparatively long (80 microns) and of a characteristic shape (Figure 1). These larvae were obtained by collecting large numbers of planktonic crustacea from the Slimbridge pens with an aquarium net, examining the animals in batches under the microscope, and selecting those infected with larvae of the required species.

The results of these experiments are shown in Table II. Both species of tapeworm grew and matured rapidly; they began producing eggs nine days after infection. At this time the largest worms were 230 mm. long and weighed 345 mg. If early growth is assumed to have been exponential over this period, these specimens of *D. coronula* doubled their wet weight in less than nine hours and their length in less than 19 hours.

After day 9, eggs continued to be produced until the worms were eliminated.

Table I. The species of tapeworm larvae found in crustacea from the Slimbridge ponds.

| Tapeworm species | Host species | | |
|------------------------------------|-------------------------|----------------------------|--------------------------|
| | <i>Cyclops strenuus</i> | <i>Cyprina ophthalmica</i> | <i>Cypridopsis vidua</i> |
| <i>Fimbriaria fasciolaris</i> | + | + | + |
| <i>Sphenacanthus</i> sp. | + | + | — |
| <i>Hymenolepis spiralibursata</i> | + | + | + |
| <i>Sobolevicanthus gracilis</i> | + | + | + |
| <i>Diorchis nyrocae</i> | + | + | + |
| <i>Nematoparataenia southwelli</i> | — | + | — |
| <i>Dicranotaenia coronula</i> | — | + | + |
| <i>Diorchis stefanskii</i> | + | — | — |

Egg production by *S. gracilis* in two birds was measured by putting the ducks in wire-mesh floored cages, collecting the faeces over a period of one week, making a suspension of the faeces in water, and counting the eggs in aliquots. The estimated totals were 24,000 and 36,000 eggs per worm per day. Elimination of whole worms with the faeces began on day 11 and continued until the infections were lost. The last specimens of *S. gracilis* were found 36 days after infection, and the last *D. coronula* 42 days after infection.

An unexplained feature of these results was the considerable variation in growth rates of worms. Within the same host, the biggest worms were often ten times heavier than the smallest. This was not due to a 'crowding effect' since the retardation of smaller worms was just as great in birds with light infections as in those with heavy ones. Further investigation of these phenomena was defeated by the technical difficulty of keeping a sufficient number of uninfected birds in the laboratory, and in obtaining viable cestode larvae in sufficient quantities at the appropriate times.

Tapeworm populations in small Mallard flocks.

Flocks of wild-type Mallard were reared under tapeworm-free conditions a mile from the Wildfowl Trust and then put into a pen at the western end of the Slimbridge enclosures. This pen contained a pond about fifteen feet in diameter. The birds picked up infections with tape-

worms by feeding on infected crustacea in the pond. These infections in the crustacea derived from wild birds visiting the pond both previously and during the experiment. Seven species of tapeworms were acquired by the birds. Each species occupied a characteristic zone of the alimentary canal; shown diagrammatically in Figure 2. Some of the Mallard were killed at intervals to determine the number and condition of their tapeworms. Two such experiments were performed.

Experiment A. (Figure 3).

Twenty-four 5-7 week old uninfected ducklings were put into the pen on 25th June 1961. Three further birds were dissected to check that they were indeed free from tapeworm parasites at this time. Four ducklings were removed from the pen after 17 days and dissected the following day. Thereafter samples of three birds were removed and dissected in cycles of 3, 9, and 27 days until day 118, when the two remaining birds were examined. The rate at which parasite populations might be expected to change was not previously known. The sampling intervals were therefore arbitrary and compromised between observing short-term population changes and providing long-term data.

Of the cestode species acquired by the birds during this experiment, three occurred only sporadically. The two commonest species, *Sobolevicanthus gracilis* and *Diorchis stefanski*, were found in respectively 12 and 17 of the 24 birds examined. The pattern of infection with

Table II. Growth and longevity of tapeworms in Khaki Campbell ducklings.

| | no. of worms | length (mm.) | | weight (mg.) | |
|---------------------------------|--------------|--------------|--------|--------------|------------|
| | | mean | range | mean | range |
| <i>Sobolevicanthus gracilis</i> | | | | | |
| day 3 | 14 | 12.5 | 6-14 | 0.5 | 0.2-0.9 |
| day 6 | 18 | 62.5 | 45-90 | 41.2 | 14.9-75.4 |
| day 9 | 10 | 69.0 | 30-105 | 91.5 | 59.4-126.4 |
| day 12 to day 33 | 44 | 59.7 | 20-125 | 34.0 | 1.2-79.2 |
| day 36 | 2 | 60.0 | 25-85 | 29.5 | 3.3-55.2 |
| day 42 | 0 | | | | |
| day 48 | 0 | | | | |
| <i>Dicranotaenia coronula</i> | | | | | |
| day 3 | 6 | 6.8 | 5-9 | 0.2 | 0.1-0.3 |
| day 6 | 10 | 97.0 | 85-120 | 41.9 | 29.5-62.8 |
| day 9 | 6 | 160.8 | 80-230 | 168.1 | 29.8-345 |
| day 12 to day 33 | 25 | 221.4 | 35-440 | 255.2 | 0.9-691 |
| day 36 | 0 | | | | |
| day 42 | 2 | 157.5 | 50-265 | 107.5 | 7.0-208 |
| day 48 | 0 | | | | |

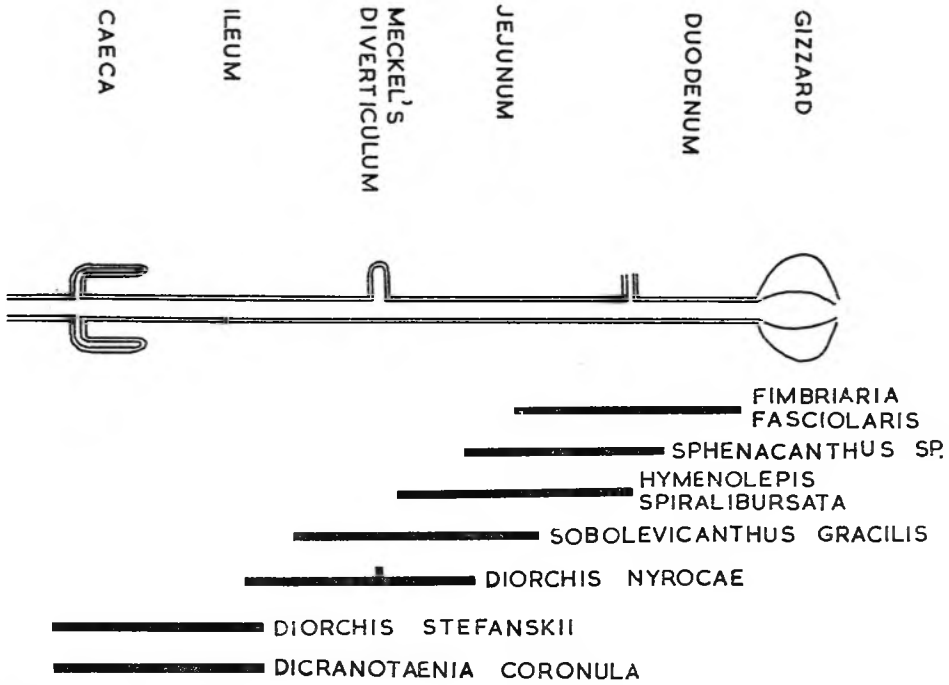


Figure 2. Zonation of tapeworms in the host gut (diagrammatic).

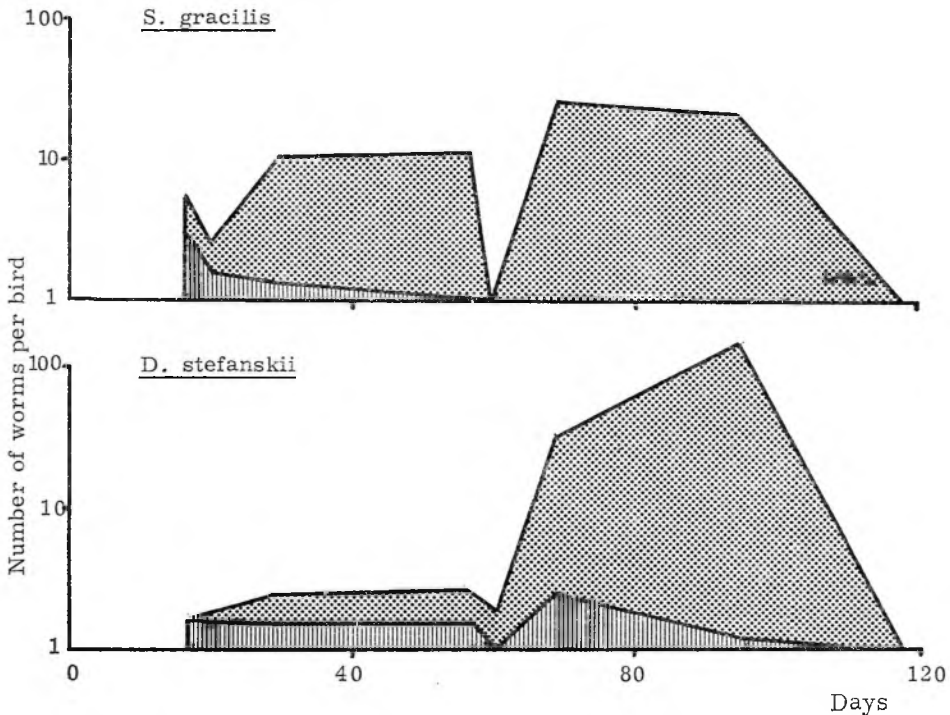


Figure 3. Mean numbers of *S. gracilis* and *D. stefanskii* (logarithmic scale) recovered from birds in Experiment A.
 Vertical bars — mature tapeworms
 Stippled — smaller immature tapeworms

both these worms was the same. A small number of large mature worms up to 190 mm. in length were found on days 17 and 20. The mean level of infection then rose, and this process accelerated by day 60. At the same time the size of the worms decreased so that most were small, stunted and immature. By the end of the experiment the mean levels of infection had fallen. These changes are shown in Figure 3, and mean lengths of specimens of *S. gracilis* in relation to the number of worms in each host are shown in Figure 4. In the other cestode species changes in infection levels and worm condition followed a similar pattern, in so far as their sporadic occurrences allowed the detection of changes.

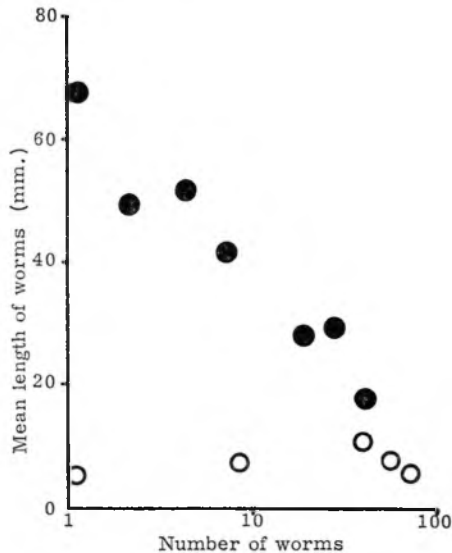


Figure 4. Experiment A. Mean lengths of *S. gracilis* from different hosts.

Black dots — 18-56 days after the birds were put in the pen
Open dots — 68-95 days after the birds were put in the pen

Experiment B. (Figure 5).

The objects of this experiment were:

i) to investigate the relationship between intermediate host populations and adult tapeworm infections in a wild-type Mallard flock over a whole summer, and

ii) to provide further information on the stunting phenomenon. The design of this experiment was more complex. A large number of uninfected birds were put into the same pen as before on 18th June 1962 and kept over the hard winter of 1962-63. On 27th February 1963 (day

258), and thereafter at 21-day intervals until 4th September, samples of four birds were put into cages in the laboratory. Their faeces were collected for 7 days, examined carefully to see if they contained any pieces of tapeworm, and then used for counts of tapeworm eggs by the dilution method. The birds were then killed and dissected. Some of the birds did not settle under these conditions and these were killed after 2-3 days without faeces having been collected.

To simulate breeding in a host flock, 22 uninfected ducklings were added to the pen on 3rd July 1963. They were accepted by the adult flock (at that time 12 birds) and became an integral part of it. Samples of four of these juvenile birds were killed after 7, 14 and 21 days, and then at the same 21-day intervals as the adults until 4th September: the remaining two were killed on 25th September. As it had been found that tapeworms could mature very rapidly in young birds, the ducklings were examined at once and not kept for faecal examination.

At the same times as each sample of ducks was removed, estimates were made of the total populations of crustacea and their parasites in the pond. This was done by sampling crustacea at four depths, using a perspex box of 500 cc. capacity, closeable at any depth. The numbers of parasite larvae were estimated by collecting crustacea with an aquarium net and counting the numbers of cysticercoid larvae of each species in 1,000 *Cyclops strenuus* and in 200 *Cypria ophthalmica*. Statistical analysis of replicates showed that the crustacea were estimated with an accuracy of $\pm 10\%$; no similar assessment of the accuracy of the cysticercoid estimates could be made.

Seven species of tapeworms were found during the course of this experiment, and all of them were found in more than a quarter of the birds. The commonest species, *S. gracilis*, was found in 39 of the 56 birds examined.

The four birds in the first sample of adults, which had been in the pen for eight months when they were removed on 27th February, were heavily infected with a mean burden of 120 worms (of 4 species) per bird. At this time it was estimated that there were 750,000 *Cyclops strenuus* and 10,000 *Cypria ophthalmica* in the pond and that the levels of cysticercoid infection in both were less than 0.5%. Subsequent changes in levels of infection of ducks and crustacea with three species of tapeworms and their larvae are shown in Figure 5. During the

summer the levels of infection in ducks remained constant, but the infection of *Cypria* with larvae of *S. gracilis* and *D. coronula* increased. By 3rd July there were 1,349,000 *C. strenuus* and 354,000 *C. ophthalmica* in the pond. The infection level in *Cyclops* was still less than 0.5% but in the ostracod *Cypria* it had risen to over 30%. Nearly all of the adult worms found in the ducks were small stunted individuals only a few millimetres in length. None of the faeces from the 20 birds kept in cages contained eggs, and even after the hosts had been in the laboratory for seven days the worms were still very small, showing that both growth and reproduction remained inhibited.

Because of the high populations of larval cestodes present, the ducklings put in the pen in 1963 quickly acquired heavy burdens of several hundred tapeworms per bird. Initially many of these worms were large mature specimens up to 100 mm. in length, but after three weeks the worms found were more and more stunted, and after six weeks were only a few millimetres in length, as were those in the adult birds. This pattern of events was similar to that observed in experiment A.

The increased input of eggs into the pond from the mature worms in the ducklings raised the level of infection until more than 50% of the *Cypria* carried cysticercoids. Since the presence of such a

larva castrates the ostracod, this had a disastrous effect on the population of the latter which was decimated from 354,000 on 3rd July to 31,000 on 14th August. This explains the drop in cysticercoid numbers which can be seen in Figure 5. *Cyclops* were much less heavily infected; by 4th September the infection rate had only risen to 1%, giving a cysticercoid population of 25,000 larvae in the pond.

These experiments demonstrate inhibition of the growth of tapeworms. This develops after ducks have been continuously exposed to a high level of infection. The maturation of worms picked up by ducklings at a time when those in adult birds were stunted shows that factors in the external environment such as the nature of the food supply were not responsible. Detailed analysis of the data for *S. gracilis*, the commonest tapeworm species, support this hypothesis. The mean lengths of worms from each host in Experiment A are shown in Figure 4. At first there was a linear relation between mean worm length and the logarithm of worm number; this was observed from day 18 to day 56 and is represented by black dots in the Figure. At this period there would seem to be a 'crowding effect' due to competition between the worms in the gut. This phenomenon is now well known in tapeworm infections in both mammals and birds (Read and Simmons 1963). After day 56 all worms

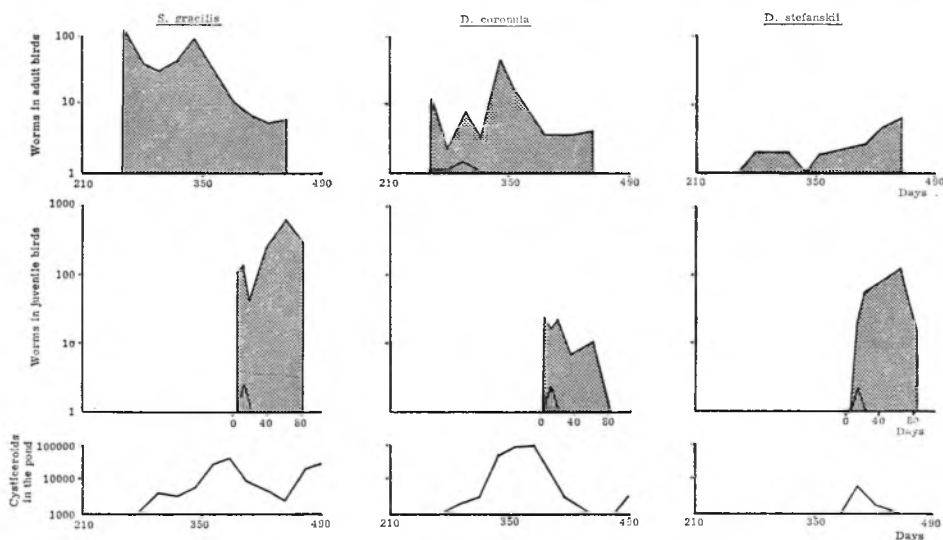


Figure 5. Experiment B. Mean numbers of *S. gracilis*, *D. coronula* and *D. stefanskii* in adult and juvenile birds, and total numbers of cysticercoid larvae of the same species.

Vertical bars — mature tapeworms

Stippled — smaller immature tapeworms

became stunted, at both high and low population densities; this is represented by open dots in the Figure. The same result was obtained for worms from the juvenile birds in Experiment B, except that at the higher population densities in this experiment, inhibition was more rapid and became marked after day 21. In the adult birds in Experiment B there was no relation between size and numbers of worms—all were stunted and no mature specimens were found.

The mechanism of this inhibition is not understood. It has often been reported that the presence of adult tapeworms in rats and other mammals may inhibit the development of any further worms which may be acquired. This phenomenon is called premunition (Roberts and Mong 1968). Since inhibition is also maintained in adult ducks with long standing infections of small worms, some kind of host response may be involved. It is very difficult to separate effects due to premunition from host response effects (for example, immunity), but this has been done in an ingenious experiment by Tan and Jones (1967). These authors surgically implanted into mice, tapeworms previously exposed to X-rays; because of the irradiation, these survived for only a few days. On reinfesting the mice with normal worms, they found that development was retarded, compared with controls, showing that the previous infection had changed the suitability of the host for tapeworm growth.

The considerable differences in growth rates of worms in ducks infected under laboratory conditions (Table II) may also be explained in terms of a host response. Worms reaching maturity in 6-14 days complete their development before a response is provoked. Slower-growing worms have not reached maturity by the time the host response occurs, and under the subsequent sub-optimum conditions are unable to satisfy the enormous energy requirements for egg production. This is entirely speculative, but demonstrates the need for further research.

Although the cause of inhibition is not known, we can consider its significance in the interaction of host and parasite populations. Wildfowl are highly mobile animals which often congregate in large numbers at certain times of the year, and disperse at others. If the fecundity of their tapeworm parasites is such that their populations can be maintained when the hosts are dispersed, then their populations would increase rapidly when the hosts congregate. Most cestodes of Anatidae are

large parasites in relation to the size of their hosts, therefore great numbers may be detrimental to the birds, and hence, in terms of survival, to the parasites themselves. Inhibition of growth therefore provides a mechanism for reducing the effects of high densities of parasites on their hosts. It also limits the rapid increase of cestode populations which would otherwise occur when the hosts congregate, by reducing the egg laying rate and increasing the time a generation takes to reach maturity. It is not known how long inhibition is maintained when parasite populations fall, and this is a first priority for further research.

Wisniewski, Szymanik and Bazanska (1958), also noted a 'crowding effect' amongst tapeworms of wild duck caught in Poland. They generalised this as a 'formation of a population structure', i.e. of tapeworms within the Anatidae of a particular region—and they speculated that this could be regarded '... as a form of defence of parasite and host, the population structure (being) convenient for both, and may be accounted for as reflecting a full accommodation of both'.

The results from sampling crustacea and their parasite larvae also showed some interesting relationships between populations of parasites, hosts and intermediate hosts. The decrease in cysticeroid numbers in midsummer, due to castration of the ostracods by the parasites themselves, is an additional mechanism by which tapeworm numbers may be regulated when the hosts are crowded.

At times when both copepods and ostracods were infected with larvae of tapeworms such as *S. gracilis* and *H. spiralibursata*, the ostracods were much the more heavily infected. This was probably a consequence of their bottom-living habit, since tapeworms eggs sink rapidly in water. Cysticeroids of *D. stefanskii* were found only in copepods; ostracods do not appear to be a suitable host for this species. The numbers of cysticeroids of *D. stefanskii* in the pond were consequently very much smaller than those of the other species (Figure 5). However, the populations of adult parasites of this species in the ducks were as large as those of others, for example *D. coronula*. This suggests that copepods are a more efficient intermediate host than ostracods, perhaps because they occur at all depths and are therefore more likely to be eaten in numbers by ducks dabbling at the surface.

Estimates of the relative infection efficiency of cysticeroids from the two types

Table III. Relative infection efficiency of tapeworm larvae. Ducklings in Experiment B.

| Tapeworm species | hosts of larvae on 3.7.63 | | relative infection efficiency (per cent) |
|--------------------------|---------------------------|----------|--|
| | ostracods | copepods | |
| <i>D. nyrocae</i> | + | — | <0.01 |
| <i>H. spiralibursata</i> | + | — | 0.01 |
| <i>D. coronula</i> | + | — | 0.01 |
| <i>F. fasciolaris</i> | + | — | 0.07 |
| <i>D. stefanski</i> | — | + | 0.11 |
| <i>S. gracilis</i> | + | + | 0.22 |

of intermediate hosts were made by comparing the mean numbers of tapeworms in the ducklings killed on day 7 in Experiment B with the cysticeroid numbers in the pond one week earlier. The results are shown in Table III. Relative infection efficiency was defined as

$$\frac{\text{number of tapeworms per bird} \times 100}{\text{number of tapeworm larvae in the pond}}$$

It can be seen that uptake was more efficient in those two species utilising copepods. From the data for infection of ducks and ostracods with *D. coronula* it was estimated that at least 12 ostracods must have been eaten each day; this is equivalent to the filtration by each duck of three-quarters of a litre of water per day. These are of course only very rough estimates, calculated on the unreal assumptions that the crustacea are evenly distributed in the pond, and that all the

cysticeroids which are eaten become adult tapeworms.

Although many of the birds in Experiment B were carrying infections of 200-300 worms, none of them showed obvious signs of any resultant ill-effects. This does not mean of course that tapeworms are never of pathological significance in wildfowl, they may well become so when the host is subjected to abnormal stress. But the present experiments have shown that the effects of the worms on their hosts under a variety of conditions need further careful experimental investigation.

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Summary

Recent work on the incidence of tapeworm infection in Anatidae and on the life cycles of the parasites is reviewed. Experiments carried out at Slimbridge on tapeworm parasites in Mallard showed that in a primary infection some of the worms may grow very rapidly to a large size, but they do not survive in the host for more than 42 days. In flocks of Mallard exposed to continuous re-infection, worm numbers built up to high levels but their growth was inhibited. The mechanism of this inhibition is not known; it probably acts as a density-dependent regulator of the total worm population. Some numerical relationships between numbers of crustacea in a pond, numbers of tapeworm larvae parasitising them, and numbers of adult tapeworms in ducks feeding on them, are described.

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