

# Long-term dynamics of *Ligula intestinalis* and roach *Rutilus rutilus*: a study of three epizootic cycles over thirty-one years

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## SUMMARY

Data are presented on 2 full epizootic cycles and the start of a third of *Ligula intestinalis* in roach *Rutilus rutilus* in a small lake, and the relationships of these cycles to the densities of rudd, *Scardinius erythrophthalmus*, and Great Crested Grebes, *Podiceps cristatus*, over 31 years. The parasite was introduced to the lake by *P. cristatus* in 1973 at a time when the roach population had increased in response to eutrophication to a level at which individual fish growth was stunted and the hitherto dominant rudd population had declined in numbers as a consequence of inter-specific competition with roach. *Ligula* prevalence peaked at 28% in only 2 years: thereafter parasite-induced host mortality caused a decline in the roach population, releasing fish from stunting and allowing the rudd population to recover. The consequent improved growth of roach individuals and their short life-span reduced *Ligula* transmission rates and prevalence levels declined to approximately 1% although *Ligula* nevertheless persisted for a further 10 years. Following a massive winter-kill of the fish populations in 1984–1985, fish and *Ligula* numbers declined to barely detectable levels and the parasite disappeared from samples. Rudd recovered first, then roach and interspecific competition again led to a decline in rudd numbers. This increase in roach numbers led to a decrease in roach growth rates, which coincided with the re-colonization of the lake by *Ligula*. This second epizootic of *Ligula* peaked within 2 years in 1991–1992, when up to 78% of roach were infected with a maximum abundance of 2.2 parasites and intensity of 21 parasites. Heavy parasite-induced mortality of roach led to a decline in numbers, an improvement in individual growth rate and a reduction of *Ligula* transmission rates such that the epizootic died out in 1996. Similar conditions of roach numbers and growth prevailed at the start of a third cycle in 1998. The course of events over the second cycle was so similar to that of the first that it confirms the interpretations of that cycle. Comparison with other localities shows that epizootics of *Ligula* always coincide with rapid increases in roach numbers, for whatever cause, and stunted growth, which together attract piscivorous birds. At the start of a cycle *Ligula* is a major determinant of the population dynamics of the roach, but at the end of the cycle the fish population dynamics determine those of the parasite. The cycles are not regulated and the roach–*Ligula* system is inherently unstable.

Key words: *Ligula*, population cycles, host–parasite systems, long-term dynamics, epizootics, instability.

## INTRODUCTION

The plerocercoid stage of *Ligula intestinalis* can survive in its cyprinid fish host, for example roach *Rutilus rutilus*, for several years, whereas the adult survives in the piscivorous bird definitive host for a few days only (Dubinina, 1980). Because of this longevity in the fish and the possibility of multiple infections, plerocercoids may attain a weight up to half of that of their fish host and so the direct and indirect effects of *Ligula* upon its roach host may be severe. These effects include suppression of gonad development and hence of fish reproduction as a consequence of the influence of the parasite on the host pituitary (Kerr, 1948; Arme & Owen, 1968; Arme, 1975, 1997; Taylor & Hoole, 1989; Hoole, 1994) which renders infected roach sterile even if

they harbour only a single *Ligula*. Other effects, in addition to pathological changes in host organs, include distortion of the fish abdomen and breakdown of counter-shading (Sweeting, 1977), alteration in host behaviour and shoaling (Orr, 1966) and change in distribution within a water body (Bean & Winfield, 1992). The effects of these changes are to increase mortality rates in infected fish, either directly by reducing their ability to survive over winter (Wyatt & Kennedy, 1988) or indirectly by making them more susceptible to predators, both bird and fish (Van Dobben, 1952; Holmes & Bethel, 1972; Sweeting, 1976; Hoole, 1994). In either case transmission of the parasite to its definitive host is facilitated as the birds prey selectively upon infected fish.

This combination of sterilizing infected fish and making them more susceptible to predation has a major impact upon the population biology of roach or any other intermediate host species (Dobson,

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1988). *Ligula* typically exhibits epizootic cycles over a period of 4–5 years. Following its arrival in a lake, often introduced by birds, prevalence rises very rapidly to attain levels close to 100%. Infected roach die and in the absence of any recruitment into the population the roach population crashes, to be followed by a decline in *Ligula* levels as transmission rates fall. This cycle has been reported from a number of localities in Britain and Ireland, including roach in Chew Reservoir (Wilson, 1971), in a gravel pit (Sweeting, 1976), in Yeadon Reservoir (Sweeting, 1977), in the Lake of Mentieth (Morrison, 1977) and in Lough Neagh (Tobin, 1986; Bean & Winfield, 1992). *Ligula* has also been held responsible for population declines in bleak *Alburnus alburnus* in the River Thames (Harris & Wheeler, 1974) and several fenland rivers (Moore & Brown, 1975). All of these studies, with the exception of those of Bean & Winfield (1992) and Winfield, Winfield & Tobin (1992), have concentrated on the *Ligula* epizootic and *Ligula*–fish interaction and they have not considered the effects of the changes in the fish population on the aquatic community of which they are part. None of them has considered what happens after the epizootic; it is never stated whether or not *Ligula* died out, but there are no reports of a second or subsequent epidemic cycle in any of the above localities. *Ligula* appears in many ways to behave like a supertramp (*sensu* Diamond, 1975): it has excellent powers of dispersal and is brought into a lake with a migratory bird, its population increases rapidly and then decreases just as rapidly, and although it may then go locally extinct it may first have been transported by a bird to a new locality. There are reports of the parasite persisting for several years in some North America lakes (Black & Fraser, 1984) and in some of the large reservoirs in Russia (Bauer & Stolyarov, 1961; Izyumova, 1987), but in none of these cases were there any detailed continuous studies of the population dynamics of the parasite and its fish host and their impact on the whole ecosystem extending over time-spans of more than 15 years.

One exception to all these generalizations is the epizootic of *Ligula* in roach in Slapton Ley, a small lake in Devon. The first cycle of *Ligula* infection has been documented by Burrough & Kennedy (1979), Kennedy & Burrough, (1981), Wyatt & Kennedy (1988, 1989) and Kennedy (1985), and the events have been interpreted as follows. In the late 1960s the lake became increasingly eutrophic and reached a hypereutrophic state by the end of the 1970s. Associated causally with the entrophication was the expansion of the roach population to a level in the early 1970s at which intra-specific competition had produced a population of small, stunted fish and inter-specific competition had led to a decline in the hitherto dominant population of rudd, *Scardinius erythrophthalmus*. The dense roach population

attracted Great Crested Grebes, *Podiceps cristatus*, to breed in the lake, and they brought with them *Ligula*. *Ligula* first appeared in 1973 and peaked at a prevalence of 28% and a mean abundance of 0.5 in 1975. The parasite caused a decline in the roach population resulting in a concomitant recovery of the rudd population, such that the parasite was then a major determinant of the population dynamics of the fish populations. As the roach population declined, intra-specific competition was reduced and fish growth rates improved. This, together with a regular alternation of good and bad roach year classes, narrowed the window for transmission of *Ligula* from copepod to fish. Transmission rates declined and levels of *Ligula* fell, so that in the late 1970s the situation was reversed and *Ligula* population levels were constrained (Wyatt & Kennedy, 1989) by the atypical population dynamics (Wyatt, 1988) of the roach. During the severe winter of 1984–1985 the lake froze over for a long period and there was a massive winter-kill of all species of fish with numbers falling to a level at which roach and rudd were not found regularly in the samples and *Ligula* disappeared (Kennedy, 1996). Even though population parameters of *Ligula* were apparently constrained at levels well below those reported from other epizootics, there was no evidence that this was due to the operation of any regulatory factors or that the *Ligula*–roach system was stable (Kennedy, 1985). Indeed, the system appeared to be inherently unstable (Kennedy & Burrough, 1981), as a number of destabilizing factors (May & Anderson, 1978) were operating on the system and parasite levels were transmission determined (Wyatt & Kennedy, 1989).

As is the case with the great majority of field studies, these interpretations could not be confirmed or refuted by experiment nor was manipulation of the system feasible. However, monitoring of the fish in the lake continued after 1985 and in late 1980s it became clear that the fish populations were starting to recover. An increase in the rudd population was followed by an increase in the roach population (Kennedy, Wyatt & Starr, 1994) and the re-appearance of *Ligula* (Kennedy, 1998). This in effect created the conditions of a natural experiment and achieved the desired manipulation of the system. Accordingly, this second epizootic of *Ligula* was studied in detail with a view to comparing it with the first cycle and testing the interpretations based on a study of that cycle. Study of the second cycle also extended the sampling period from 15 to 31 years, thus providing a unique long-term data set for a fish parasite system that exceeds the 13 to 19 year durations of the few other such long-term sets (Smith, 1973; Esch *et al.* 1986; Kennedy, 1993, 1997). There have been some preliminary and incomplete reports of the second cycle (Kennedy *et al.* 1994; Kennedy, 1996, 1998), but the aims of this

present paper are (1) to describe the complete second cycle and part of the third in detail, (2) to determine whether events in the second cycle confirm interpretations of the first, and (3) to present the whole data set from 1970 to 2000 and to explain the apparent persistence of the parasite in the light of what is known about the lack of regulation and instability of the *Ligula*–roach system.

#### MATERIALS AND METHODS

A full description of Slapton Ley is given by Burt & Heathwaite (1996) (and in other papers in this special volume of Field Studies). In summary, the Ley is a very small (0.7 km<sup>2</sup>), isolated, freshwater, coastal lagoon of recent (1000 year) origin, comprising 2 former lagoons and impounded from the sea by a shingle barrier. The Lower Ley is an open lake, approximately 3 km long and with a maximum depth of 2.5 m, whilst the smaller Higher Ley is almost completely covered by floating vegetation. The system is fed by a river entering the Higher Ley and it discharges directly into the sea from the Lower Ley. The fishery comprises roach, rudd, perch *Perca fluviatilis*, pike *Esox lucius* and eels *Anguilla anguilla*, and occasional trout *Salmo trutta*. It is unmanaged, but has changed following changes in land use in the catchment and has been subject to eutrophication (Kennedy, 1996).

The fishery has been sampled continuously since 1970, using gill nets, seine nets, traps and electric fishing as appropriate to season and conditions. Methods of fish capture, examination and ageing and of examination for *Ligula* are described by Burrough & Kennedy (1979), Kennedy & Burrough (1981), Wyatt & Kennedy (1988, 1989) and Wyatt (1988). Intensity of sampling of necessity varied throughout the period from monthly samples in some years to only one or two samples a year in others. Samples were seldom fully representative of the fish populations as it was never possible to sample all age classes of fish on each occasion and all methods are selective. Rudd, for example, were probably underestimated in the samples in all seasons except autumn.

Roach population sizes are expressed as catch per unit effort (cpue), in this case as catch per unit fishing day. Roach year class strengths were estimated by the method of Kempe (1962), and roach growth is expressed as the mean length of fish at the end of each year of life, their birthday being taken as the first of June. Terminology for parasites accords with the definitions of Bush *et al.* (1997), and the variance to mean ratio of abundance is used as a measure of overdispersion. Data on infection levels are presented as far as possible for the life-span of each roach year class, and by calendar year with all year classes combined. Parasite impact on roach is

measured by the Parasite Index (PI) (Arme & Owen, 1968; Wyatt & Kennedy, 1988; Hoole, 1994) during a peak year of the second epizootic in 1991. The data set on the second cycle extends from 1987 to 2000. Finally, this set is combined with data from the first cycle and the population crash to produce a 31-year continuous data set.

A copy of all raw data sets will be deposited in the archives of the Slapton Ley Field Centre, operated by the Field Studies Council.

#### RESULTS

##### *The second cycle*

*Roach population dynamics.* Roach virtually disappeared from the samples from September 1984 (the last sample before the population crash) until September 1990. A few fish were caught irregularly in the years 1986–1989 (Table 1A). Rudd were the first species to recover from the crash and their numbers peaked in 1990; thereafter their numbers declined and their occurrence in the samples became erratic. From 1987 to 1990 the roach:rudd ratio favoured rudd (Table 1A). Although several roach were caught by anglers in 1989, they did not appear in numbers in the samples until 1990. Their numbers peaked in 1991, and the roach to rudd ratio switched in favour of roach thereafter. The values of cpue were high in 1991, 1998 and 1999 and low in 1994, suggesting the existence of good and bad year classes. The estimates of year class strength (Table 1B) confirm the existence of a strong year class in 1991 and further suggests a poor one in 1988 and a weak one in 1992. Between 1986 and 1993 there is a suggestion of alternating good and bad year classes. The methodology for calculating year class strengths relies upon sampling being representative of all age classes, and this was not normally the case from 1994 onwards. However, inspection of the cpue (Table 1A) suggests that there may have been a very weak year class in 1994 and a less weak one in 1997, whereas there were good year classes in 1998 and especially in 1999.

The mean length of roach at the end of each year of life can be used as an index of crowding and intra-specific competition. Roach had resumed breeding from 1987 onwards, although few were taken in the samples between 1987 and 1989 (Table 2), as evidenced by the appearance of fish of the 1987–1989 year classes in samples taken in 1990–1993 (Table 3). The length of 2+ roach of the 1988 and 1989 year classes gives no indication of unusually good or bad growth. However, there was a decline in the size of 0+ fish of the 1991 and 1993 year classes (Table 2), evident also when they were 1+. This would suggest some overcrowding and stunting around this time. This was clearly alleviated in the 1994 year class, as

Table 1. Summary parameters of the roach and rudd populations in Slapton Ley for the period after their population crash

(A) Sampling effort		1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Roach numbers		0	1	2	72	263	235	175	29	174	137	149	177	276	50
Days fished		3	3	1	2	4	5	4	2	4	3	4	2	3	1
Cpue*		0	0.3	2	36	66	47	44	15	43	44	37	88	92	50
Rudd numbers		120	8	76	348	32	22	33	0	39	0	0	65	0	0
Roach/rudd		0	0.12	0.03	0.2	8.2	10.7	5.3	-	1.1	-	-	2.1	-	-
(B) Roach year class strengths		1986	1987	1988	1989	1990	1991	1992	1993						
Year class		81	102	45	109	96	159	62	90						
Relative strength†		81	102	45	109	96	159	62	90						

\* Catch per unit effort, in this case per standard day's fishing.

† Values are relative to 100 (see Kempe, 1962).

average size at the end of all 3 years was high. Growth of roach then declined again to a nadir in 0+ fish in 1999 and in 1+ fish of the 1998 year class i.e. in the calendar year 1999 indicating an increase in intra-specific competition at this time. Growth rates were inversely correlated with year class strengths, which were good in 1991, 1998 and 1999 and poor in 1994.

*Ligula population dynamics.* *Ligula* first re-appeared after the fish and parasite population crash in 1990, in a 2+ fish of the 1988 year class (Table 3). It then appeared in 1991 in a 4+ fish of the 1987 year class. On both these occasions only a single fish was infected, prevalence in the age class was low (< 10%) and parasite dispersion was random. The new epizootic cycle appears to have commenced in 1991, when roach of the 1989, 1990 and 1991 year classes were infected. Prevalence levels had soared to 78% and abundance to 2.24 in 1+ fish of the 1990 year class. Maximum intensity of infection was 9 in roach of the 1989 year class, multiple infections were commoner than single ones and the variance to mean ratio reached 3.25 in 2+ fish. In 1992 prevalence levels were still high (71% in 1+ roach), mean abundance had increased to 3.9 in 3+ fish, and multiple infections were still common, especially in 3+ fish where maximum intensity reached 21 and overdispersion peaked at 4.8. In this year fish of all ages from 0 to 4+ were infected. By 1993 infection levels were starting to fall; maximum prevalence was now 53% and abundance 0.9 in 1+ roach, multiple infections were less common with a maximum intensity of 4 in 2+ fish, although overdispersion was still high at 4.2 in 3+ fish. In 1993 4+ fish were no longer infected. This rise and decline is more clearly evident when data are summarized by calendar year (Table 4). The second cycle started in 1990, reached its peak in 1992 and declined from 1993 to 1994. Both the build up and decline were very rapid and in the peak years fish of all ages, not just young ones, were infected.

There was a slight resurgence of infection in 1995 in 1+ and 2+ fish (Tables 3, 4), but levels of infection fell again between 1996 and 1998. In this latter year infections were found in 0+ fish and infection levels rose again in 1999 and 2000. In 1+ fish of the 1999 year class prevalence had attained 71% and abundance 1.1, with a maximum intensity of 3.0. Dispersion remained random for each group of roach, but rose slightly above 1 when all year classes were combined (Table 4). This would appear to be the start of a third cycle, and fish of ages 0, 1 and 2 years old were infected. Levels of infection in the third cycle were lower than those in the second, as prevalence per year never exceeded 14% nor abundance 0.2 and dispersion was close to random (Table 4). Prevalence levels in individual age groups (71.4% in 1+ roach of the 1999 year class)

Table 2. Mean length (mm) (+s.d.) of roach at the end of each year of growth for the period after the population crash

(Figures in parentheses are sample sizes. Data are given for first 3 years of life only.)

Year class	0+	1+	2+
1987	N.S.	N.S.	N.S.
1988	N.S.	N.S.	132.0+14.0 (18)
1989	N.S.	N.S.	123.1+7.0 (31)
1990	64.4+5.9 (5)	102.2+9.9 (16)	129.2+8.9 (9)
1991	52.3+7.6 (18)	98.4+6.3 (15)	129.5+9.6 (21)
1992	60.0 – (3)	93.2+7.4 (14)	N.S.
1993	51.5+5.2 (11)	N.S.	127.7+4.3 (8)
1994	74.2+2.8 (5)	112.1+5.0 (16)	154.9+11.7 (11)
1995	72.1+8.3 (30)	100.8+6.1 (8)	134.2+6.8 (22)
1996	54.5+7.0 (44)	78.4+10.8 (19)	144.5+11.9 (25)
1997	51.0 – (1)	N.S.	N.S.
1998	46.5+5.5 (46)	64.2+1.9 (5)	123 – (2)
1999	42.8+7.2 (40)	93.7+6.8 (7)	N.S.
2000	43.4+4.1 (41)	N.S.	N.S.

N.S., Not sampled.

approached those of the second cycle, but abundance values were always lower, multiple infections were never common and intensity never exceeded 3.0.

Considering the cycles as a whole, the peak years of the second cycle, 1991 and 1992, co-incided with and followed closely on a year with a strong year class of roach (1991) (Table 1B) when fish were stunted and growth had declined (Table 2). Similarly, the rise in infection levels in the third cycle in 1999 and 2000 coincided with and followed closely on years with strong year classes of roach in 1998 and 1999. By contrast, zero infection levels in 1994 coincided with a very weak year class of roach in that year (Table 1A) and maximum growth of 0+ fish (Table 2).

*Impact of Ligula on roach.* The impact of *Ligula* on roach as measured by the parasite index is shown in Table 5 for 1991 at the peak of the second cycle. In every month, both mean and maximum index values declined from 1+ to 2+ fish: this may reflect death of more heavily infected fish or a lower transmission rate to older fish. In September the PI values increased from 0+ to 1+ fish, but declined thereafter. The impact of the parasite increased from July to September within each age group of roach, and overall the greatest impact of the parasite was on the 1+ group in September. Highest maximum values, of 40+, were also reported from August and September.

Both mean and maximum PI levels were always higher in roach carrying multiple infections, regardless of age or month, with the difference being most pronounced in 1+ fish. PI values are not shown for other years as the same patterns are evident. Thus, the impact of the parasite was lower in the third cycle because multiple infections were far less frequent and maximum intensity was far

lower. What is clear is that at the time of the peak of the epizootic in the second cycle *Ligula* was having a severe impact on infected fish.

*The long-term changes in Ligula and roach populations.* The complete 31-year data set is shown in Fig. 1, to facilitate comparison between the 3 cycles. The courses of events throughout the 3 cycles are very similar indeed. Roach became overcrowded and stunted in growth between 1971 and 1973; *Ligula* first appeared in the latter year and the epidemic peaked 2 years later in 1975. Roach growth was poor from 1991 to 1993, *Ligula* appeared in 1990 and the epidemic increased in 1991/1992, 1 to 2 years later. In the third cycle roach became stunted in 1998, and *Ligula* levels increased within 2 years. *Ligula* induced mortality of roach from 1975 onwards reduced the pressure of intra-specific competition and so growth rates of *Ligula* improved whilst transmission declined and prevalence, abundance and maximum intensity fell. The same pattern was evident in the second cycle; as roach growth rate improved from 1993 to 1995, all infection parameters declined. All population parameters of *Ligula* were highest in the second cycle compared to the first, where prevalence never exceeded 30%, abundance 0.5, or maximum intensity 5.0 and where dispersion was always close to random except at the peak in 1975. The first cycle lasted 9 years, from 1973 to 1982; it is impossible to know if the slight rise in prevalence in 1984 heralded the start of a new cycle as the population was eliminated in the ensuing crash of the fishery. The second cycle lasted 6 years, from 1990 to 1996, and the length of the third cycle is not known. In many respects the parameters of the third cycle are more similar to those of the first rather than to those of the second cycle. Overall, however, the data show that epizootics of *Ligula* can re-occur



Table 4. Occurrence and density of *Ligula* in roach, summarized by calendar year, for the period after the population crash

(All year classes combined and only fish up to and including 3+ considered.)

Year	<i>n</i>	Prevalence	Abundance	Variance	Variance/mean
1986	0	0	0	0	0
1887	0	0	0	0	0
1988	1	0	0	0	0
1989	2	0	0	0	0
1990	67	1.5	0.015	0.015	1
1991	213	48.3	1.52	2.13	1.4
1992	198	52.0	1.94	9.36	4.82
1993	148	33.1	0.59	1.04	1.77
1994	13	0	0	0	0
1995	173	16.8	0.183	0.181	0.99
1996	126	1.6	0.016	0.016	1
1997	143	1.4	0.014	0.014	1
1998	175	2.3	0.022	0.022	1
1999	276	10.7	0.123	0.152	1.23
2000	50	14.0	0.220	0.379	1.72

Table 5. Summary parameters of the Parasite Index (PI) of roach in 1991

	All infections			Single infections			Multiple infections		
	Mean + s.d.	<i>n</i>	Max	Mean + s.d.	<i>n</i>	Max	Mean + s.d.	<i>n</i>	Max
July									
1+	12.0+8.1	10	24.4	6.3+3.2	4	10.3	15.8+8.2	6	24.4
2+	4.6+4.5	9	13.7	3.1+3.5	6	9.0	7.8+5.3	3	13.7
August									
1+	15.2+11.6	12	42.5	9.3+8.2	7	22.9	23.5+11.1	5	42.5
2+	11.0+5.4	23	19.6	5.4+2.9	8	9.5	14.1+3.8	15	19.6
September									
0+	8.6+3.0	12	13.0	7.3+2.6	8	11.7	11.3+1.5	4	13.0
1+	23.4+9.6	14	42.5	15.3	2	20.8	24.6+9.6	12	42.5
2+	16.1+11.1	13	45.1	3.5	2	5.5	18.4+10.4	11	45.1

within a single locality over a long time-span, and that the course of each epidemic is remarkably similar.

#### DISCUSSION

The interpretation of long-term data sets always faces the problem of consistency in sampling methodology and effort over time. These problems are accentuated in fishery data because sampling is never completely representative; each method of sampling is selective to some extent and even when the same methods are employed local weather and other physico-chemical conditions can prevent some age classes of fish from being represented in the samples. A further complication is that it is very difficult to obtain truly representative samples of *Ligula* levels, because the parasite alters the behaviour of fish and infected fish may shoal together in particular parts of

a lake (Orr, 1966). There is general agreement (Sweeting, 1976, 1977; Morrison, 1977; Burrough & Kennedy, 1979; Kennedy & Burrough, 1981) that single samples may give an imprecise measure of *Ligula* infection levels. It is advisable therefore to always take several samples and to look at general trends in long-term data sets rather than focus on any particular sample.

The second cycle of *Ligula* in roach of Slapton Ley followed on the recovery of the fish populations from the crash due to winterkill in 1984–1985, and the condition of the roach population in 1990 was very similar to that in the early 1970s at the start of the first cycle. Prior to the 1970s, rudd were the dominant cyprinids in the Ley and the roach population was very small (Burrough, Bregazzi & Kennedy, 1979). The increase in the roach population was associated with increasing eutrophication of the lake, and the concomitant decline in the rudd population was believed to be a direct result of

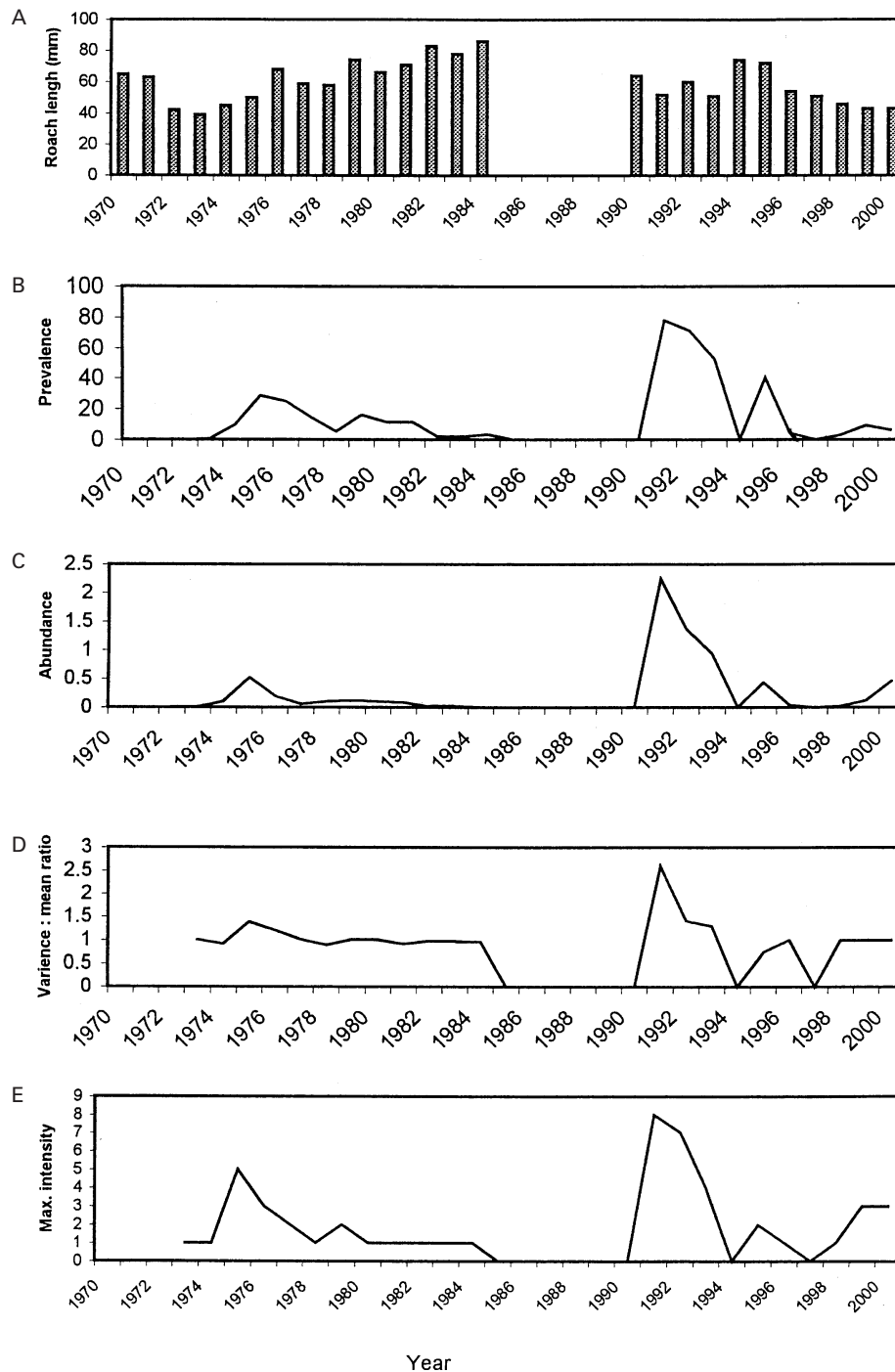


Fig. 1. Annual changes in the growth rate of roach and of infection parameters of *Ligula* for the complete period of sampling. (A) Mean length of 0+ roach at the end of their first year. (B) Maximum prevalence of *Ligula* in 0+/1+ roach. (C) Maximum mean abundance of *Ligula* in 0+/1+ roach. (D) Maximum variance to mean abundance ratio of *Ligula* in 0+/1+ roach. (E) Maximum intensity of *Ligula* in 0+/1+ roach. s.d. values are omitted for clarity. No data are presented for the period 1985–1989 inclusive as sample sizes were too small and unrepresentative to provide valid estimates. Data from Kennedy (1985), Kennedy *et al.* (1994), Kennedy (1996) and this paper.

competition from the roach. This interpretation was confirmed by events in the second cycle. Rudd were the first species to recover after the winterkill crash, and they reached high densities but then started to decline as soon as roach re-appeared. In the first cycle, roach numbers increased further to produce a very dense population as a consequence of strong

year classes in 1972 and 1973 and this accelerated stunting in growth and accentuated intra-specific competition (Burrough & Kennedy, 1979). A dense population, a strong year class in 1991 and a reduction in growth rate were also evident at the start of the second cycle, and indeed similar conditions were evident at the start of the third cycle.



The dense roach population in the early 1970s attracted Great Crested Grebes (*Podiceps cristatus*) to the lake, and they bred there for the first time post-war in 1973 (Elphick, 1996), bringing with them *Ligula* (Kennedy & Burrough, 1981). The grebe population increased rapidly to 5 or so breeding pairs in the 1970s, rising to 7 or 8 pairs in some years. Following the fish crash, numbers of grebes declined rapidly to a single breeding pair in 1985 and then slowly recovered to reach 5 breeding pairs again by 1990 and the population continued to increase to a peak in 1994–1995 (Elphick, 1996). Thus, at the start of each cycle there was a dense population of stunted roach, low numbers of rudd and a large grebe population. These were ideal conditions for the transmission of *Ligula*, as small roach fed on plankton for longer periods than larger ones, and so levels of parasite prevalence and abundance rose very rapidly to a peak within 2 years of its appearance.

Conditions of a strong roach year class, roach stunting and high *Ligula* prevalence characterized the first phase of each cycle. The second phase was characterized by parasite-induced roach mortality, both direct over winter (Wyatt & Kennedy, 1988) and indirect by predation. This mortality alleviated the overcrowding within the roach population and the relaxation in intra-specific competition allowed roach growth rates to improve: conditions of a poor year class and subsequent improved roach growth were evident in 1974 and 1994. The decrease in roach numbers allowed an increase in rudd and so the roach to rudd ratio declined in both cycles. The changes in the roach population dynamics after the first cycle, and in particular the rapid growth, which reduced the time fry spent feeding on copepods, and the alternation of good and bad year classes, reduced transmission rates of *Ligula* to roach and so prevented the parasite population levels building up again (Wyatt & Kennedy, 1988, 1989). Decline of *Ligula* levels in the second cycle also coincided with improved roach growth rates in 1994 and 1995 and a decline in roach numbers in 1994 and there is some indication of alternation of good and bad years over the period 1990–1995. Overall, therefore, the courses of the second, and as far as it was observed, the third cycles are very similar to that of the first, with similar conditions prevailing at times of rising and falling infection levels. In the first part of each cycle *Ligula* determined the dynamics of the roach population, but in the second the situation was reversed and the roach dynamics determined the *Ligula* infection levels.

There are of course some differences between the cycles, although these are less significant than the similarities. In the second cycle, the roach to rudd ratio was never as highly in favour of roach as it was in the first cycle. This is almost certainly due to the rapid increase in *Ligula* to much higher levels of

prevalence and abundance than in the first cycle. The roach population growth was checked before numbers rose to very high levels, and the parasite appears to have had a greater impact on roach in the second cycle as PI values were higher than those reported for first one (Kennedy & Burrough, 1981; Wyatt & Kennedy, 1988). This was related to the greater frequency of multiple infections and it can therefore be presumed that *Ligula* had a greater effect on more fish in the second cycle than in the first. Prevalence and abundance levels in the second cycle were far higher than in the first. It is not immediately clear why this should be so, but it may relate to abundance of zooplankton. During the period of the winterkill and low fish densities, predation on zooplankton must have been greatly reduced and it is likely that copepod populations were very much larger after several years of low fish numbers. This would have had the effect of widening the transmission window for *Ligula* from copepod to fish host. *Ligula* levels in the third cycle were on the whole more similar to those of the first cycle than to those of the second; this may reflect the facts that there was no massive expansion of the roach population in the late 1990s such as occurred in the early years of the decade and in the early 1970s, and also by then the copepod populations had again suffered several years of fish predation. Causal relationships between *Ligula* levels, plankton abundance and fish feeding on plankton have been commented upon in several other *Ligula* epizootics (Wilson, 1971; Harris & Wheeler, 1974; Sweeting, 1976; Morrison, 1977; Bean & Winfield, 1992).

The interpretations in this study have thrown some light on the conditions necessary for *Ligula* epizootics in general. These occurred in the Ley when roach populations were expanding rapidly, regardless of the cause of the expansion which was associated with eutrophication in the 1960s and recolonization in the 1990s. Such a roach population expansion also seems to be a feature of many *Ligula* epizootics elsewhere. In Lough Neagh, the roach expansion followed its introduction into the lake in 1973 and the lake was also characterized by abundant zooplankton (Tobin, 1986; Bean & Winfield, 1992). This expansion of the roach population in the lough was also causally associated with an expansion of the Great Crested Grebe population as was the case in Slapton Ley, but in Lough Neagh this led to a reduction in other bird species, especially of Tufted Duck *Athya fuligula* (Winfield *et al.* 1992). Elsewhere *Ligula* epizootics followed hard upon use of reclaimed gravel pits for recreation and development of the roach fisheries therein (Sweeting, 1976, 1977), or occurred in the early years following reservoir formation, generally 2–3 years after flooding, when both fish and copepod populations were expanding (Bauer & Stolyarov, 1961; Izyumova, 1987). The epizootic in Chew reservoir was associated with re-

colonization of the reservoir by roach following earlier exclusion of coarse fish at the time of flooding (Wilson, 1971).

The duration of a *Ligula* epizootic appears to be determined primarily by local conditions, especially plankton density and roach feeding habits. As smaller roach, whether younger or stunted, feed more intensively on plankton than larger ones, highest levels of *Ligula* prevalence and abundance are generally found in the smaller fish (Arme & Owen, 1968; Harris & Wheeler, 1974; Sweeting, 1976, 1977; Morrison, 1977; Bean & Winfield, 1992). However, when infection levels are very high as in the second cycle in Slapton Ley, fish of all ages may be infected although abundance is still generally higher in smaller fish. The decline in the roach population is due to parasite-induced mortality which in turn may be caused by poor survival of heavily infected fish (those with a high PI) over winter (Wyatt & Kennedy, 1988) or to selective predation by fish such as pike *Esox lucius* (Sweeting, 1976) or birds such as grebes or cormorants *Phalacrocorax phalacrocorax* (Van Dobben, 1952). Sterility of infected fish means that recruitment into the roach population falls, and a disappearance of young fish due to the failure of a year class is a common feature of the decline phase of a *Ligula* cycle (Moore & Brown, 1975; Sweeting, 1976) and in the Ley in 1994. The changes in the population structure of roach may be extensive; for example, in Lough Neagh the cpue of roach fell from 100 in 1985 to <10 three years later in 1988 and no young fish were recruited into the population which became exclusively composed of old fish (Bean & Winfield, 1992). Similarly, in Chew Reservoir cpue fell from 6600 in 1966 to <10 in 1969, following the epizootic of *Ligula* which peaked in 1965 (Wilson, 1971). The link between infection levels and plankton and roach mortality was particularly evident in this reservoir, as part of the reservoir was cut off by a dam from the main body and in this pool roach fed on benthos, there were no *Ligula* infections and roach numbers did not decline over the period of the epizootic in the main reservoir. The length of an epizootic will also depend on the parasite impact, generally measured by the PI. In Slapton Ley, PI values were higher in the second cycle than the first, and this cycle was shorter than the first. Higher maximum intensities of *Ligula* in roach have been reported from other localities e.g. 63 from Chew (Wilson, 1971), 53 from Thryberg and 29 from Ravensthorpe (Arme & Owen, 1968), but mean PI levels from the second cycle in Slapton are of a similar order of magnitude to those reported from these and other localities (Sweeting, 1976, 1977).

Whilst many authors describe the declining phase of a *Ligula* epizootic, there is no clear picture of what happens thereafter. Most accounts relate to short periods only covering the peak of infection e.g. for 10

months (Sweeting, 1976), for 1 year (Harris & Wheeler, 1974), for 3 years (Morrison, 1977; Bean & Whitfield, 1992) or for 6 years (Wilson, 1971). None of these authors report a further epizootic, or state that the parasite disappeared from the locality and a second cycle has never been reported from these localities by any other author. This may reflect the fact that no further studies were carried out there; however, there does seem to be a tacit assumption that the parasite disappears when roach population levels fall below a critical threshold. The first cycle at Slapton Ley was already the single longest documented *Ligula* cycle, 12 years, at the time of the fish kill. There are indications that *Ligula* can persist for at least 10 years in some of the larger Russian reservoirs e.g. the Rybinsk Reservoir (Izyumova, 1987), although here the focus of the infection shifted within the reservoir. Persistence will also be influenced by the identity of the fish intermediate host; if the parasites infect bream *Abramis brama*, which may live much longer than roach, there will be long time lags in the system and the *Ligula* will survive longer in the lake. It is possible therefore that *Ligula* may indeed be endemic in very large water bodies, but in small water bodies the impression is that it behaves as a supertramp (Diamond, 1975). It possesses excellent powers of dispersal. It is adapted to, associated with, and widely dispersed by, migratory, piscivorous birds (Dubinina, 1980) and it generally colonizes new lakes by their activities. If conditions are suitable, it increases in numbers rapidly, decimates or wipes out the roach population (Wilson, 1971; Sweeting, 1976; Winfield & Bean, 1992) and then becomes locally extinct. However, propagules may have been moved on to a new locality by birds before extinction.

The situation in Slapton Ley where the parasite appears to have persisted for almost 30 years and underwent 3 infection cycles is unique, and is pertinent to ask why this should be so. Such persistence is all the more surprising when, as has been argued previously by Kennedy & Burrough (1981) and confirmed by Wyatt & Kennedy (1989), the *Ligula*-roach system there is fundamentally unstable with parasite levels being transmission determined. Using the criteria of Anderson & May (1978) and May & Anderson (1978), the system is characterized by destabilizing factors. These include (i) parasite effects on host reproduction, (ii) absence of any density-dependent host mortality, (iii) failure of hosts killed by *Ligula* to be taken out of the system, (iv) time lags in the system and (v) parasite dispersion close to random for much of the course of an epizootic. There is no evidence that any of these are compensated for by density-dependent factors. The declining levels of the parasite during the first cycle were not due to regulation but to a decline in roach numbers and parasite transmission rates (Wyatt & Kennedy, 1988, 1989). It is impossible to

know what would have happened if the fish populations had not crashed. The parasite persisted for 9 years after the peak of the epizootic, albeit at very low levels for the last 3 years, but prevalence had actually increased slightly in September 1984, immediately before the crash, and there is no indication that it was about to disappear. It is not clear whether the parasite survived in the lake from 1984 to 1990 in the small relict population of roach in the Higher Ley and continued to cycle through the few Great Crested Grebes that remained, or whether its re-appearance when the roach population was recovering was due to a re-introduction to the lake with Grebes (Kennedy, 1998). No infected roach were found over this period, although catches were so small that this can have no significance, but on balance the evidence favours a re-introduction (Kennedy, 1998). A natural re-colonization of a lake by *Ligula* following disappearance of its fish host, in this case by poisoning, and subsequent recovery after 8 years has been reported by Black & Fraser (1984) in Crevice Lake. In this lake there were clearly 2 distinct cycles of *Ligula* rather than 1 continuous one over 18 years. In Slapton Ley, the second cycle was clearly a response to the population dynamics of the roach when recovering from the crash, which set up the ideal conditions for a new epizootic. In that sense it was a local response to the particular conditions of this locality. It may therefore be more correct to regard the first and second cycles as essentially independent of each other and a reflection of the particular changes in the catchment. If so, the persistence of *Ligula* in Slapton Ley over almost 30 years is more apparent than real. The first cycle persisted for 12 years; the second for 7 years and the duration of the third is unknown. The study has therefore shown that 1 cycle of *Ligula* can be followed by another, but it is no longer necessary to explain how the parasite could persist in an unregulated system for 28 years; it did not. The very few other long-term studies on parasite–host systems have also failed to provide any evidence that regulatory factors played a part in parasite persistence. They suggest rather that habitat conditions have a powerful influence on parasite populations. As Esch *et al.* (1986) pointed out, long-term trends in parasite populations should follow one of two patterns. Consistency in parasite population parameters could be due to stability of climatic, physico-chemical and biotic conditions in a habitat or to the operation of density-dependent mechanisms. Inconsistency is the result of environmental perturbation, habitat change or variability in the behaviour of host populations, which may in turn reflect environmental variability. The system they studied, in Gull Lake, was inconsistent and parasite levels largely reflected changes in the trophic condition of the lake. The system studied by Kennedy & Rumpus (1977) was consistent; it was suggested that this may have

been due to the operation of regulatory factors but it is equally likely that it can be attributed to stability of the physico-chemical conditions. The dynamics of the diplostomatid eyefluke populations in fish in Slapton Ley were also strongly affected by the fish population crashes (Kennedy, 2001) and the studies on this lake together with the studies of Smith (1973) and Tinsley (1999) have demonstrated clearly the impact that catastrophic climatic changes or habitat and host perturbations can have on the long-term dynamics of parasite populations.

The *Ligula*–roach system in Slapton Ley is at the same time unique and deceptive; it appears to exhibit linked host and parasite cycles which together with persistence over 28 years suggests tight population regulation. The importance of the present study lies in revealing the deception by showing that the first and second cycles are independent events and that neither the cycles nor persistence need to be attributed to regulation: they are the results of inconsistency and reflect habitat changes. Appearances here are indeed deceptive; something that could only be revealed by a unique continuous long-term sampling programme and a fortuitous natural experiment. It is likely that *Ligula* host dynamics will vary over short and long terms in other, especially larger, lakes in relation to differences in habitat conditions and their changes, but confirmation of this will require further long-term studies of the parasite and its hosts. Such studies of this and other parasites should now have a very high priority.

Over the period of 31 years too many people have helped to be able to list them all individually. Nevertheless, we must single out R. P. Troake, then Warden of Slapton Ley Field Centre, for initiating this study and subsequent Wardens and staff of the Centre and thank them for their continual support and for use of their facilities. Financial support has been provided at various times by the NERC, SERC, Exeter University Research Fund and the Whitley Wildlife Conservation Trust, to each of whom thanks are also due. R. J. Burrough, P. R. Bregazzi, R. J. Wyatt and K. Starr have also played major roles in understanding the fish–parasite relationships in Slapton Ley.

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