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Source: *The Journal of Animal Ecology*, Vol. 43, No. 3 (Oct., 1974), pp. 821-837
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/3538
Accessed: 19/09/2008 15:13

THE RELATIONSHIP OF *CHAETOGASTER LIMNAEI* (OLIGOCHAETA: NAIDIDAE) WITH A VARIETY OF GASTROPOD SPECIES

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INTRODUCTION

Two subspecies of *Chaetogaster limnaei* (von Baer) are recognized: *C. l. limnaei* (von Baer) inhabits the outer surfaces of its gastropod host and *C. l. vaghini* Gruffydd is found in the renal organ (Gruffydd 1965).

Many authors have recorded *C. l. limnaei*, either in studies of the worm itself or of its relationship with trematode populations, in British species of gastropod in genera such as *Acroloxus*, *Ancylus*, *Lymnaea*, *Physa* and *Planorbis*, and in foreign species in genera such as *Australorbis*, *Biomphalaria*, *Bulinus*, *Helisoma*, *Lymnaea*, *Melanoides*, *Physa*, *Physopsis* and *Segmentina*. The subspecies *Chaetogaster limnaei vaghini*, although not always recognized as such, has been recorded by fewer authors, and only in *Lymnaea* and *Physa* (Buse 1968).

Observations on *Chaetogaster limnaei* in the pond at the University College of North Wales, Bangor, in which *Lymnaea stagnalis* (L.) and *L. peregra* (Müll.) were the dominant gastropod species, showed that *Chaetogaster limnaei vaghini* occurred only in the former and *C. l. limnaei* solely in the latter. This suggested that the worm might be able to differentiate between various species of gastropod, and it was therefore decided to examine the behavioural relationship of *C. limnaei*, collected from a wide range of gastropod species, with its host. Setal lengths were also studied, to determine whether any morphological differences were apparent.

THE OCCURRENCE OF *CHAETOGASTER LIMNAEI*

Gastropods were collected from twenty ponds or lakes in Caernarvonshire and Anglesey in North Wales, and Shropshire and Cheshire in England. Each of the twenty-one species of snail collected was examined for both subspecies of *Chaetogaster*. The species of snail found in each locality and the percentage infected with *C. limnaei* are shown in Table 1. *Lymnaea peregra* was the most frequent snail, being found in thirteen of the localities, followed by *Potamopyrgus jenkinsi* (Smith) in eleven.

Chaetogaster limnaei limnaei was found to infect eighteen of the twenty-one species examined. One hundred per cent infection was recorded in *Physa fontinalis* (L.), of which a total of thirty-eight specimens from five localities was examined, and also in *Planorbis corneus* (L.). The one specimen of *Succinea* examined was also infected. Fifty per cent or more of the specimens were infected in ten of the gastropod species found. The larger snail species, *Lymnaea stagnalis*, *Planorbis corneus*, *Lymnaea peregra* and *L. palustris* (Müll.), had the greatest mean number of worms per snail, as did *Bithynia tentaculata* (L.). A specimen of *Lymnaea peregra* contained the greatest population, 144 individuals,

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Table 1. *The gastropods found in twenty localities and the percentage infected with* Chaetogaster limnaei limnaei *and* C. l. vaghini (*values only shown when snail is present;* C. l. vaghini *values in parenthesis*)

Localities, with grid references

Gastropod species	College Pond SH 577719	Mill Pond SH 652726	Llanllechid SH 636693	Llyn Sisi SH 640693	Vaynol 1 SH 541694	Vaynol 2 SH 541693	Beaumaris Reservoir SH 584750	Llangefni Reservoir SH 442774	Llyn Coron SH 378700	Llyn Hendref SH 398766	Pentre Berw SH 462723	Birchgrove Pool SJ 435233	Blake Mere SJ 418338
Acroloxus lacustris (Linn.)	.	.	.	.	.	.	.	.	.	50	.	.	.
Ancylus fluviatilis (Müll.)	.	.	.	.	.	.	.	.	.	.	.	.	.
Bithynia leachi (Sheppard)	.	.	.	.	.	.	.	.	.	.	.	*100	.
B. tentaculata (L.)	.	.	.	.	.	.	.	.	.	.	.	100	0
Lymnaea auricularia (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.
L. palustris (Müll.)	.	.	.	.	.	.	100	.	.	0	.	.	.
L. peregra (Müll.)	93	100	100	66	. (69)	100	.	.	33	25	.	100	.
L. stagnalis (L.)	0 (68)	.	.	.	.	.	.	.	.	.	.	*100	.
L. truncatula (Müll.)	.	.	.	.	.	.	*100	.	.	*100	.	.	.
Physa fontinalis (L.)	.	.	.	.	.	.	100	.	*100	.	.	.	.
Planorbis albus (Müll.)	.	.	.	.	0	.	.	.	.	.	0	67	.
P. carinatus (Mull.)	.	.	.	.	.	.	.	.	.	.	.	100	.
P. contortus (L.)	.	.	.	.	.	.	67	.	0	.	0	.	.
P. corneus (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.
P. planorbis (L.)	.	.	.	.	.	.	.	.	.	.	.	50	.
P. vortex (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamopyrgus jenkinsi (Smith)	0	37	.	.	0	.	.	0	0	0	.	.	.
Segmentina complanata (Linn.)	.	.	.	.	.	.	.	.	.	.	50	.	.
Succinea sp.	.	.	.	.	.	.	.	*100	.	.	.	.	.
Valvata cristata (Müll.)	.	.	.	.	7	.	.	.	.	.	.	.	.
V. piscinalis (Müll.)	.	.	.	.	0	.	.	.	86	.	.	.	.

Gastropod species	Cole Mere SJ 435329	Crose Mere SJ 431307	Newton Mere SJ 424344	The Mere Ellesmere SJ 404348	White Mere SJ 418329	Wirral 1 SJ 325814	Wirral 2 SJ 330804	No. of localities containing gastropod	No. of snails examined	Percentage of snails infected	Mean no. of worms per snail	Range of no. of worms
Acroloxus lacustris (Linn.)	0	.	.	0	.	.	.	2	4	0	.	.
Ancylus fluviatilis (Müll.)	0	.	.	75	.	.	.	3	41	20	0·8	0–10
Bithynia leachi (Sheppard)	0	.	.	*100	.	.	.	3	4	50	6·0	0–23
B. tentaculata (L.)	80	17	.	100	*100	.	.	6	22	59	16·9	0–85
Lymnaea auricularia (L.)	.	.	.	0	0	.	.	2	4	0	.	.
L. palustris (Müll.)	.	.	.	.	.	.	.	2	4	75	14·8	0–32
L. peregra (Mull.)	100 (25)	0	100	80	14	.	.	13	89	67 (16)	15·2 (0·8)	0–144 (0–8)
L. stagnalis (L.)	0	.	.	.	.	100 (83)	.	4	8	75 (63)	19·3 (37·0)	0–63 (0–116)
L. truncatula (Müll.)	.	.	.	.	0	.	.	3	4	50	4·5	0–17
Physa fontinalis (L.)	100	*100	100	.	.	.	.	5	38	100	9·9	1–26
Planorbis albus (Müll.)	*100	.	17	0	.	.	.	6	20	15	0·3	0–2
P. carinatus (Müll.)	63	40 (20)	.	13	0	.	.	5	29	48 (3)	2·4 (0·3)	0–12 (0–1)
P. contortus (L.)	.	.	33	.	.	.	.	4	14	21	0·3	0–2
P. corneus (L.)	.	.	.	.	.	100	100	2	9	100	19·2	1–36
P. planorbis (L.)	.	.	.	.	0	.	.	1	2	0	.	.
P. vortex (L.)	0	0	.	0	.	.	.	4	33	9	0·2	0–3
Potamopyrgus jenkinsi (Smith)	50	6	0 (*100)	0	9	.	.	11	181	23 (0·6)	0·2 (0·06)	0–3 (0–1)
Segmentina complanata (Linn.)	.	.	.	.	0	.	.	2	3	67	0·3	0–1
Succinea sp.	.	.	.	.	.	.	.	1	1	100	1·0	1
Valvata cristata (Müll.)	.	.	.	.	.	.	.	1	14	7	0·7	0–1
V. piscinalis (Müll.)	100	0	.	.	.	.	.	4	37	32	2·4	0–11

* Only one snail examined.

followed by *Bithynia tentaculata* with eighty-five and *Lymnaea stagnalis* with sixty-three.

Chaetogaster limnaei vaghini, however, was found in only four of the twenty-one species of snail (Table 1): this included one individual in each of *Potamopyrgus jenkinsi* and *Planorbis carinatus* (Müll.). The percentage infection, in parentheses in Table 1, and the total population were greatest in *Lymnaea stagnalis*. (The values for *L. stagnalis* from the College Pond are omitted as an intensive study (Buse 1971) involved the examination of approximately 1200 individuals.)

BEHAVIOURAL STUDIES

It had previously been shown by 'choice' experiments that *Chaetogaster limnaei* was attracted to the egg masses and to the mucous trail left by the host snail (Buse 1972). This suggested a method by which the worms found the general area of the host. By use of an apparatus presenting two streams of water, it was demonstrated that the worms were attracted to chemical substances from the host and that, when this 'host-factor' (Davenport 1950) was present, they tended to move upstream, and thus towards the source.

The snails used in the following experiments were obtained from the sources shown in Table 2.

Table 2. *The source of the gastropods used in experiments*

Gastropod species	Source
Lymnaea peregra	College Pond; Cole Mere; Llanllechid
L. stagnalis	College Pond; Wirral 1
Physa fontinalis	Beaumaris Reservoir
Planorbis corneus	Wirral 1
Potamopyrgus jenkinsi	Mill Pond

The specificity of C. limnaei *to its own host*

As *C. limnaei* had been shown to be attracted to its host, it was of interest to investigate the possibility that *Chaetogaster* from a particular species of snail could detect and accumulate on its own host in preference to other gastropod species. Four types of 'choice' experiment were employed, presenting worms from a specific source with non-infected snails, egg masses, mucous trails or 'host-factor' of several gastropod species.

Non-infected snails

Non-infected specimens of *Lymnaea peregra*, *L. stagnalis* and *Planorbis corneus* were obtained by laboratory culture from the eggs (Buse 1968). In each 'choice' experiment, four specimens of each of these three species were introduced into a 30 cm diameter plastic bowl, with a water depth of 5 cm: aeration and artificial food were supplied. Thirty specimens of the relevant subspecies of *Chaetogaster limnaei* were added after 7 days, and the distribution of these between the snails determined after a further 7 days. An equal distribution between the snail species would suggest that the attraction to each was equal. The increase in worm numbers during some of the experiments was due to asexual reproduction.

The first two experiments involved the introduction of *C. l. limnaei* from *Lymnaea peregra*. The resultant distribution (Table 3) shows that the worms were equally distributed between *L. peregra* and *Planorbis corneus*, but did not infect *Lymnaea stagnalis* to any

Table 3. *The attachment of* Chaetogaster limnaei *from several sources to non-infected* Lymnaea peregra, L. stagnalis *and* Planorbis corneus

Chaetogaster limnaei subspecies	Source	Distribution of worms after 7 days		
		Lymnaea peregra	*L. stagnalis*	*Planorbis corneus*
C. l. limnaei	*Lymnaea peregra*	18	0	11
C. l. limnaei	*L. peregra*	15	1	14
C. l. limnaei	*Planorbis corneus*	19	1	23
C. l. vaghini	*Lymnaea stagnalis*	1	0	0
C. l. vaghini	*L. stagnalis*	0	2	0

extent. To determine whether this result was due to *L. stagnalis* being repellent, the experiment was repeated with *L. stagnalis* only, resulting in thirty-nine worms attaching in one experiment and six in another. The experiments with *Chaetogaster limnaei limnaei* from *Planorbis corneus* also resulted in *Lymnaea peregra* and *Planorbis corneus* being heavily infected. The corresponding experiments with *Chaetogaster limnaei vaghini* resulted in one worm infecting *Lymnaea peregra* in the first, and two infecting *L. stagnalis* in the second.

The results show that there was differential infection of the species of snail, but there was no indication of host-specificity.

Egg masses

Each experiment consisted of two egg masses from the host species of snail and two from a different species arranged alternately in a plastic petri-dish of 85 mm diameter and with a water depth of 8 mm. A minimum of thirty of the relevant *Chaetogaster* were introduced, the exact number depending on availability, and the experiment left in the dark. After 24 h, the distribution of the worms between the egg masses was examined, the null hypothesis being an equal distribution between the two types.

The results (Table 4) show that in the 8 experiments with *C. limnaei limnaei*, the number of worms on the host's egg masses was significantly greater than expected in Expts 3, 4 and 6, there being no significant departure from the expected equality in Expts 1, 5, 7 and 8, and the opposite in Expt 2. *C. l. vaghini* from *Lymnaea stagnalis* showed significant accumulation on its host's egg masses in both experiments.

Thus the egg mass experiments showed a degree of specificity with some of the *Chaetogaster* and hosts used.

Mucous trails

The apparatus used for the mucous trail experiments consisted of an 85 mm diameter petri-dish, containing an 8 mm depth of water, divided into six segments by a 'Perspex' separator. With the latter in position, specimens of *Lymnaea peregra*, *L. stagnalis*, *Planorbis corneus*, *Physa fontinalis* and *Potamopyrgus jenkinsi* were introduced into separate segments, greater numbers of the smaller species of snail being used in an attempt to equalize the quantity of mucus deposited. The remaining segment was left empty as a control. The position of each snail species was determined by the use of random number tables (Fisher & Yates 1957) and this was changed in subsequent experiments. The snails were left in position for 30 min. The snails and the separator were then removed, approximately fifty of the relevant *Chaetogaster* introduced, the exact number depending on availability, and the experiment left in the dark for 24 h. Each experiment was repeated eight times.

Table 4. *The accumulation of* Chaetogaster limnaei *from various sources on the egg masses of the host species and other gastropod species*

Expt no	*C. limnaei* subspecies and source	Egg masses presented	No. of worms on egg masses after 24 h	χ^2	
1	*C. l. limnaei*	*Lymnaea peregra*	25	0·3	NS
	Lymnaea peregra	*L. stagnalis*	29		
2	*C. l. limnaei*	*L. peregra*	18	40·9	***
	Lymnaea peregra	*L. stagnalis*	82		
3	*C. l. limnaei*	*L. peregra*	65	15·7	***
	Lymnaea peregra	*Planorbis corneus*	27		
4	*C. l. limnaei*	*Lymnaea peregra*	46	26·7	***
	Lymnaea peregra	*Planorbis corneus*	8		
5	*C. l. limnaei*	*Lymnaea peregra*	17	0·1	NS
	Lymnaea peregra	*Physa fontinalis*	15		
6	*C. l. limnaei*	*Planorbis corneus*	26	18·2	***
	Planorbis corneus	*Lymnaea peregra*	3		
7	*C. l. limnaei*	*Planorbis corneus*	28	1·7	NS
	Planorbis corneus	*Lymnaea peregra*	19		
8	*C. l. limnaei*	*Physa fontinalis*	12	0·3	NS
	Physa fontinalis	*Lymnaea peregra*	15		
9	*C. l. vaghini*	*L. stagnalis*	22	4·5	*
	Lymnaea stagnalis	*L. peregra*	10		
10	*C. l. vaghini*	*L. stagnalis*	26	5·2	*
	Lymnaea stagnalis	*L. peregra*	12		

Significance levels: *$P<0·05$;; ***$P<0·001$; NS not significant.

The accumulated resultant distributions of *C. limnaei limnaei* and *C. l. vaghini* from each source are shown in Table 5: in each case, the distribution between the mucous types was significantly different from equality. In each experiment, the number of worms on the host mucus was compared with the number on each of the other mucous types by calculating χ^2.

An examination of the distribution of *C. l. limnaei* from *Lymnaea peregra* showed significant aggregation on the mucus of the host, except in the comparison with the accumulation on the mucus of *Planorbis corneus*. The latter exception corresponds with the result of the non-infected snail experiments. An additional set of experiments, restricting the choice to the mucus of *Lymnaea peregra* and *Planorbis corneus*, resulted in a significant accumulation (140: 99) on the mucus of *Lymnaea peregra*. In the experiments with *Chaetogaster limnaei limnaei* from *Physa fontinalis* and *Chaetogaster limnaei limnaei* from *Planorbis corneus* (Table 5), the accumulation on the host's mucus was significant in all cases.

The experiments with *Chaetogaster limnaei vaghini* from *Lymnaea stagnalis* also resulted in significant aggregation on the host mucus in most comparisons, but an equal distribution on the mucus of *L. peregra*. An experiment presenting the 'choice' of mucus from *L. stagnalis* and *L. peregra* gave the same result (194:191).

The results of the mucus experiments show that, in the majority of comparisons, preferential accumulation of *Chaetogaster* occurred on the mucus of the host snail. This demonstrates a tendency towards host-specificity in the presence of a variety of mucous trails.

Table 5. *The accumulation of* Chaetogaster limnaei *from various sources on five types of mucus* (χ^2 *of difference between the accumulation on the host mucus and a different mucus type in brackets*)

Expt no.	*C. limnaei* subspecies and source	Accumulation on mucus types after 24 hr: *Lymnaea peregra*	*L. stagnalis*	*Planorbis corneus*	*Physa fontinalis*	*Potamopyrgus jenkinsi*	none	χ^2
1	*C. l. limnaei* *Lymnaea peregra*	119	50 (28·2)***	101 (1·5) NS	89 (4·3)*	42 (36·8)***	51 (27·2)***	67·7***
2	*C. l. limnaei* *Physa fontinalis*	89 (9·5)**	70 (20·6)***	80 (14·1)***	135	67 (22·9)***	40 (51·6)***	62·1***
3	*C. l. limnaei* *Planorbis corneus*	50 (10·5)**	30 (28·5)***	88	24 (36·6)***	40 (18·0)***	52 (9·3)**	54·5***
4	*C. l. vaghini* *Lymnaea stagnalis*	112 (0·2) NS	106	77 (4·6)*	62 (11·5)***	51 (19·3)***	54 (16·9)***	45·4***

Significance levels: *$P<0·05$; **$P<0·01$; ***$P<0·001$; NS not significant.
Each result is the total of eight experiments.

'Host-factor'

The two-water-stream 'trough' experiment, in which it had previously been shown that *C. limnaei* accumulated in the stream from the reservoir containing the host in preference to that from the other with water only (Buse 1972), was used with a different species of snail in each of the two reservoirs. The results (Table 6) show that *C. l. limnaei* from *Lymnaea peregra*, *Physa fontinalis* and *Planorbis corneus* each accumulated in significantly greater numbers in the stream containing 'host-factor' from the gastropod species from which they had been collected. *Chaetogaster liminaei vaghini* from *Lymnaea stagnalis* showed a similar result. Thus some degree of host-specificity was shown by *Chaetogaster limnaei* from the sources examined.

The results of similar experiments (Table 6), in which the worms from one host were presented with a 'choice' of water only and a stream from a snail species different from that of their own host, showed that the latter was chosen. Any gastropod species is therefore better than none.

Host-specificity and the number of gastropod species in a locality

It might be expected on *a priori* grounds that *C. limnaei* from a locality with several species of snail would have a greater degree of host-specificity than individuals from water bodies with only a single species of snail, where a response to gastropods in general would be all that was required for host location. To investigate this hypothesis, experiments were performed with *C. l. limnaei* from *Lymnaea peregra* collected from Llanllechid, with one gastropod species present, College Pond, with two species present, and Cole Mere, with many species.

The results of an experiment presenting three species of non-infected snail showed that there was virtually no accumulation on *L. stagnalis*. No significant difference was apparent between the accumulation on *L. peregra* and *Planorbis corneus* by *Chaetogaster liminaei limnaei* from Llanllechid (29 : 35) or College Pond (33 : 25), although a greater proportion from the latter accumulated on *Lymnaea peregra*, but *Chaetogaster limnaei limnaei* from *Lymnaea peregra* collected at Cole Mere showed significant accumulation on *L. peregra* (15:5). This indicated that the specificity of *Chaetogaster limnaei limnaei* was greater in a locality containing a variety of gastropod species.

The results of the mucous trail experiments (Table 7) indicated no significant difference from equality in the distribution between the mucous types of *C. l. limnaei* from Llanllechid. The *C. l. limnaei* from the two other sources showed a significant aggregation on the *Lymnaea peregra* mucus in the majority of cases.

A greater degree of host-specificity in the *Chaetogaster* from the localities with several species of gastropod is therefore suggested in both experiments.

It was also possible that a certain species of snail from different localities might vary: thus, in a 'choice' between the host snail and the same species from another locality, preference might be shown for the former. To determine whether such differences could be detected, a 'choice' of mucous trails from *Lymnaea peregra* from Llanllechid, College Pond and Cole Mere were presented. The results (Table 8) show that a significant difference in accumulation only occurred in the case of *Chaetogaster limnaei limnaei* from Cole Mere. This suggests that it was only where there were many species of snail that host-specificity was sufficiently discriminating to detect differences between the mucus of *Lymnaea peregra* from various sources. Trough experiments gave a similar result (Table 9), although *Chaetogaster limnaei limnaei* from College Pond also showed a significant accumulation in the stream from *Lymnaea peregra* from its own source.

Table 6. *The distribution of* Chaetogaster limnaei *from various sources between* (*a*) *a stream containing the 'host-factor' and a stream from another gastropod species, and* (*b*) *a stream from the other species and of water only*

C. limnaei subspecies and source	(a) Accumulation in host stream and in stream from other gastropod species: No. of exps	Accumulation after 3 h		χ^2	(b) Accumulation in stream from other gastropod species and in water: No. of exps	Accumulation after 3 h		χ^2
C. l. limnaei *Lymnaea peregra*	7	*Lymnaea peregra* 110	*L. stagnalis* 52	20·8***	3	*L. stagnalis* 89	water 17	48·9***
C. l. limnaei *Physa fontinalis*	7	*Physa fontinalis* 103	*L. peregra* 59	11·9***	3	*L. peregra* 83	water 15	47·2***
C. l. limnaei *Planorbis corneus*	4	*Planorbis corneus* 97	*L. peregra* 21	48·9***	4	*L. peregra* 54	water 22	13·5***
C. l. vaghini *Lymnaea stagnalis*	7	*Lymnaea stagnalis* 93	*L. peregra* 53	11·0***	5	*L. peregra* 48	water 27	5·9*

Significance levels: $*P<0{\cdot}05$; $***P<0{\cdot}001$.

Table 7. *The distribution, of* Chaetogaster limnaei limnaei *collected from* Lymnaea peregra *from three sources, on the mucus of various gastropod species* (χ^2 *of difference between accumulation on* L. peregra *mucus and a different mucus in brackets*)

Source of *C. l. limnaei* from *Lymnaea peregra*	Distribution on mucus types after 24 h *L. peregra*	*L. stagnalis*	*Planorbis corneus*	*Physa fontinalis*	*Potamopyrgus jenkinsi*	None	χ^2
Llanllechid	24	20 (0·4) NS	29 (0·5) NS	15 (2·1) NS	21 (0·2) NS	15 (2·1) NS	7·0 NS
College Pond	119	50 (28·2)***	101 (1·5) NS	89 (4·3)*	42 (36·8)***	51 (27·2)***	67·7***
Cole Mere	31	20 (2·4) NS	17 (4·1)*	18 (3·5) NS	11 (9·5)**	13 (7·4)**	13·5*

Significance levels: $*P<0·05$; $**P<0·01$; $***P<0·001$; NS not significant. Results are the total of four experiments.

Table 8. *The distribution, of* Chaetogaster limnaei limnaei *collected from* Lymnaea peregra *from three localities, on the mucus of* L. peregra *from each of these sources*

Source of *C. l. limnaei* from *Lymnaea peregra*	Distribution between mucus types after 24 h Llanllechid	College Pond	Cole Mere	χ^2
Llanllechid	39	45	39	0·6 NS
College Pond	33	31	33	0·1 NS
Cole Mere	31	27	61	17·4***

Significance levels: $***P<0·001$; NS not significant.

Table 9. *The distribution, of* Chaetogaster limnaei limnaei *collected from* Lymnaea peregra *from three localities, between a water-stream from* L. peregra *from its own source and from* L. peregra *from a different source*

Source of *C. l. limnaei* from *Lymnaea peregra*	Distribution of worms after 3 h between streams from *L. peregra* from two sources		χ^2
	Llanllechid	College Pond	
Llanllechid	70	79	0·5 NS
	College Pond	Llanllechid	
College Pond	87	21	40·3***
	Cole Mere	College Pond	
Cole Mere	32	8	14·4***

Significance levels: $***P<0·001$; NS not significant.

Thus, a difference between *L. peregra* from several sources can be detected and the degree of host-specificity of *Chaetogaster limnaei limnaei* was most highly developed where a number of snail species was present.

The nature of the reaction of C. limnaei *to its host*

To determine whether conditioning or genetic factors, or a combination of both, was responsible for the specificity to the host, *C. limnaei* were introduced for a period of time (7 days or 1 month) into bowls containing non-infected specimens of snails of a different species from the host. At the commencement of the experiment, the specificity of worms removed from the same source was tested by a non-infected snail experiment to determine the initial reaction to the host. This was repeated with the experimental worms at the end of the relevant period of time. If accumulation continued to occur on the original host species, specificity might be genetic, whereas if it occurred on the new host, it was probably due to conditioning.

Table 10 shows that *C. l. limnaei* from *Lymnaea peregra* still accumulated on *L. peregra* after 7 days on *Planorbis corneus*. After 1 month, however, the majority attached to *P. corneus*: this suggests that conditioning had taken place. The results of experiments with *Chaetogaster limnaei limnaei* from *Planorbis corneus* were inconclusive.

Table 10. *The distribution of* Chaetogaster limnaei limnaei *on non-infected snails after a period of time on a gastropod species other than the host*

Original host gastropod of *C. l. limnaei*	Immediate origin of *C. l. limnaei*	Distribution on snails after 7 days		χ^2
		L. peregra	*Planorbis corneus*	
Lymnaea peregra	Direct from *L. peregra*	129	29	63·3***
	After 1 week on *Planorbis corneus*	87	25	34·3***
		L. peregra	*P. corneus*	
L. peregra	Direct from *L. peregra*	129	29	63·3***
	After 1 month on *Planorbis corneus*	6	33	18·7***
		L. peregra	*P. corneus*	
Planorbis corneus	Direct from *P. corneus*	31	19	2·9 NS
	After 1 week on *Lymnaea peregra*	15	29	4·5*

Significance levels: $^*P<0{\cdot}05$; $^{***}P<0{\cdot}001$; NS not significant.

The previous 'non-infected' snail experiments did not demonstrate that *Chaetogaster limnaei limnaei* was host-specific, whereas other experiments did. It is possible that, if differential accumulation of *Chaetogaster* was due to conditioning, specificity would be apparent only in the short term experiments. The crowded experimental conditions compared with the natural situation, or the appearance of a new generation of worms by asexual reproduction (Buse 1968) could both affect the results of long term experiments.

MORPHOLOGICAL STUDIES

The most important features used in differentiating between the two subspecies of *Chaetogaster limnaei* are the length and number of setae in each bundle (Gruffydd 1965). The number of setae in the setal bundles of segments II, VI, VII and VIII and the length of setae in one bundle of each segment were therefore determined in 12 specimens of *C. limnaei* from each of several localities and several gastropod species. This resulted in approximately 100 measurements in the worms from each source. A comparison was made between the results for worms from one species of snail, but a variety of localities, and between worms from one locality, but several gastropod species.

The setae of C. l. limnaei

The mean length, with confidence limits, of the setae of each setal bundle of *C. l. limnaei* from each source was calculated (Table 11). A comparison of the means shows that variation occurred between *Chaetogaster* from different snail species in the same habitat and the same species from different habitats. To determine whether this difference was statistically significant, the ratio '*d*' was calculated for pairs of means and compared

Table 11. *The mean length of setae in segments II, VI, VII and VIII of* Chaetogaster limnaei limnaei *from several sources (length of setae in μ, ± 95% confidence limits)*

Source of *C. l. limnaei*	Mean length of setae in segments II	VI	VII	VIII
Lymnaea peregra College Pond	76·4±1·7	50·2±0·8	50·3±0·6	49·5±0·7
L. peregra Llanllechid	83·2±2·3	52·7±0·7	53·2±0·5	53·3±0·7
L. peregra Cole Mere	82·0±1·9	54·4±1·0	54·5±0·5	54·1±0·6
L. stagnalis Wirral 1	76·8±2·3	54·4±0·7	54·0±0·8	53·1±0·7
L. truncatula Beaumaris	78·4±1·8	50·4±0·5	49·4±0·5	49·5±0·6
Physa fontinalis Beaumaris	78·3±1·6	51·6±0·7	50·6±0·5	50·1±0·6
Planorbis corneus Wirral 1	74·5±1·9	52·6±0·9	51·0±1·1	47·9±1·0
Potamopyrgus jenkinsi Mill Pond	70·6±2·0	47·4±0·7	47·3±0·6	47·5±0·6

at the 5% level of probability with the value resulting from the null hypothesis that, assuming normal distribution, the difference between the means was zero (Bailey 1959). Table 12 shows the results of the comparison of the means of the setal lengths in segment II: it can be seen that that of *C. limnaei limnaei* from *Lymnaea peregra* from College Pond was significantly different from that for the same host in Cole Mere or Llanllechid, but those from Llanllechid and Cole Mere were not significantly different from each other. No difference was apparent in worms from two hosts in each of Wirral and Beaumaris. Table 13 compares the means of the setal lengths in segment VI: the means for segments VII and VIII are not compared as the setae have similar lengths. The table shows that the mean for segment VI was significantly different in worms from *L. peregra* collected from three localities. Similarly, there is a significant difference between the setal lengths of *Chaetogaster* from *Lymnaea truncatula* (Müll.) and *Physa fontinalis* at Beaumaris, and between those from *Lymnaea stagnalis* and *Planorbis corneus* in Wirral. The mean number of setae found in each setal bundle from segment II to VIII of *Chaetogaster limnaei limnaei* is shown in Table 14, together with the range in each case. The frequent loss of setae, especially from segment VI, which is the principal bundle by which the worm clings to the host (Gruffydd 1963), precluded the calculation of significant differences between the number of setae in the bundles of worms from various sources. It would seem that ten or eleven is the basic number, this being reduced by setae becoming

Table 12. *A comparison of the means of the lengths of the setae in segment II of* Chaetogaster limnaei limnaei *from each of several sources with the lengths from the other sources*

Source of *C. l. limnaei*	*Potamopyrgus jenkinsi*	*Planorbis corneus*	*Physa fontinalis*	*Lymnaea truncatula*	*L. stagnalis*	*L. peregra* Cole Mere	*L. peregra* Llanllechid
Lymnaea peregra College Pond	4·4***	1·5 NS	1·6 NS	1·6 NS	0·3 NS	4·4***	4·7***
L. peregra Llanllechid	8·3***	5·8***	3·4***	3·2**	3·9***	0·8 NS	
L. peregra Cole Mere	8·3***	5·5***	2·9**	2·7**	3·5**		
L. stagnalis Wirral 1	4·0***	1·5 NS	1·1 NS	1·1 NS			
L. truncatula Beaumaris	5·8***	3·0**	0·1 NS				
Physa fontinalis Beaumaris	6·0***	3·0**					
Planorbis corneus Wirral 1	2·8**						

Value = '*d*'; significance levels: $^{**}P<0{\cdot}01$; $^{***}P<0{\cdot}001$; NS not significant.

Table 13. *A comparison of the means of the lengths of the setae in segment VI of* Chaetogaster limnaei limnaei *from each of several sources with the lengths from the other sources*

Source of *C. l. limnaei*	*Potamopyrgus enkinsi*	*Planorbis corneus*	*Physa fontinalis*	*Lymnaea truncatula*	*L. stagnalis*	*L. peregra* Cole Mere	*L. peregra* Llanllechid
Lymnaea peregra College Pond	5·4***	4·0***	2·6***	0·4 NS	7·9***	6·6***	4·9***
L. peregra Llanllechid	11·2***	0·2 NS	2·5*	5·6***	3·4***	2·8**	
L. peregra Cole Mere	11·7***	2·6**	4·7***	7·3***	0·05 NS		
L. stagnalis Wirral 1	14·3***	3·0**	5·8***	9·3***			
L. truncatula Beaumaris	7·1***	4·2***	2·7**				
Physa fontinalis Beaumaris	8·6***	1·9 NS					
Planorbis corneus Wirral 1	9·1***						

Value = '*d*'; significance levels: $^{*}P<0{\cdot}05$; $^{**}P<0{\cdot}01$; $^{***}P<0{\cdot}001$; NS not significant.

Table 14. *The mean number of setae and range (in brackets) in the bundles of segment II, VI, VII and VIII of* Chaetogaster limnaei limnaei *from several sources*

Source of *C. l. limnaei*	Mean number of setae in segments II	VI	VII	VIII
Lymnaea peregra College Pond	9·6 (7–10)	8·2 (4–11)	9·3 (5–11)	10·3 (9–11)
L. peregra Llanllechid	10·2 (10–11)	9·8 (4–11)	10·5 (5–11)	10·4 (9–11)
L. peregra Cole Mere	9·3 (6–11)	8·8 (7–11)	9·8 (7–11)	10·8 (10–12)
L. stagnalis Wirral 1	10·0 (9–11)	7·8 (4–9)	9·7 (7–11)	9·9 (9–11)
L. truncatula Beaumaris	9·7 (9–10)	8·7 (8–10)	10·5 (10–11)	10·5 (10–11)
Physa fontinalis Beaumaris	9·4 (8–10)	8·5 (5–11)	10·2 (6–11)	10·5 (9–11)
Planorbis corneus Wirral 1	8·6 (4–10)	7·6 (3–10)	8·4 (5–10)	7·8 (6–10)

torn out, and that the number of setae in the bundles of *C. l. limnaei* from various sources appears to be more or less constant.

The setae of C. l. vaghini

Specimens of *C. l. vaghini* were collected from *Lymnaea stagnalis* in two localities only, and the mean length of the setae in segments II, VI, VII and VIII determined (Table 15). A substantial difference was apparent in segment VI, suggesting that there

Table 15. *The mean length of the setae in segments II, VI, VII and VIII of* Chaetogaster limnaei vaghini *from two sources (length of setae in* μ, $\pm$ *confidence limits)*

Source of *C. l. vaghini*	Mean length of setae in segments II	VI	VII	VIII
Lymnaea stagnalis College Pond	60·3 ± 2·4	46·2 ± 1·5	47·5 ± 1·0	47·4 ± 1·1
L. stagnalis Wirral 1	60·3 ± 1·6	42·4 ± 0·7	41·9 ± 1·0	42·3 ± 1·3
Difference between means of segment II and VI	0·3 NS	23·2***		

Value = '*d*'; significance levels: ***$P < 0·001$; NS not significant.

Table 16. *The mean number of setae and range (in brackets) in the bundles of segment II, VI, VII and VIII of* Chaetogaster limnaei vaghini *from several sources*

Source of *C. l. vaghini*	Number of setae in segments II	VI	VII	VIII
Lymnaea stagnalis College Pond	5·9 (5–7)	4·0 (3–6)	5·1 (5–7)	5·7 (4–7)
L. stagnalis Wirral 1	6·4 (4–7)	6·0 (4–7)	6·2 (6–7)	6·4 (5–7)

was variation in the worms from the different sources, but there was no significant difference in segment II.

The number of setae in these segments was also compared (Table 16). A statistical comparison was again precluded by the loss of setae, but six and seven were the most common numbers of setae in bundles of the worms from both sources.

DISCUSSION

Animals are usually found in the sort of places that are proper to their species (Andrewartha 1961). The reasons for this are, of course, complex and depend on a combination of such parameters as dispersal, behaviour, other species, and physical and chemical factors (Krebs 1972).

The distribution of the two subspecies of *Chaetogaster limnaei* on the various gastropod species in the twenty lakes showed that there was some selectivity of place to live. This was confirmed by the tendency of worms to accumulate on their own host species when presented with a 'choice' of several types of snail.

Various methods are used in the location of the place to live. These are perhaps most marked, or most apparent, in parasite/host and commensal/host relationships. Examples of relevant parasite/host relationships include the attraction of the miracidia of the trematode *Schistosoma japonicum* Katsurada to the mucous trail of the host species of snail (Faust 1924; Faust & Meleney 1924) and the accumulation of miracidia on the egg masses of the host snail and on gels impregnated with various chemical substances (MacInnis 1965). Examples from commensal/host relationships are the attraction to the chemical 'host-factor' of various polynoid species (Davenport 1950, 1955; Davenport & Hickok 1951) and of shrimps (Ache & Davenport 1972).

Previous studies of the behaviour of *Chaetogaster limnaei* (Buse 1972) have suggested that the general area of the host is found by attraction to the egg masses and mucous trail, but the final location is by reaction to chemical substances emanating from the host, with water currents providing orientation. The present study shows that this reaction is extremely sensitive: *C. limnaei* shows a 'preference' for the egg masses, mucous trail and chemical 'host-factor' from its own host species of snail.

For this degree of specificity to occur, there must be some advantage to the worms. The most obvious benefit for *C. l. limnaei* would be in maintaining the infection of the larger species of snail: these will have the greatest ciliary action, thus supplying the greatest amount of food (shown by Gruffydd (1965) to consist of diatoms, algae, Protozoa, rotifers and cercaria larvae), and allowing room for the development of population size. The advantages of host size were indicated by the largest species of snail, *Lymnaea peregra*, *L. stagnalis*, *L. palustris* and *Planorbis corneus*, containing the greatest actual and mean number of individuals of *Chaetogaster limnaei limnaei*. *Bithynia tentaculata* is an exception in that, being a ciliary feeder, it provides an ideal situation for *Chaetogaster limnaei limnaei*: this species also supported a large population.

The size of the host species is also likely to be critical for *C. l. vaghini*, which inhabits the renal organ. Thus, *Lymnaea stagnalis*, which had the largest renal organ, contained the greatest population of this worm. Confirmation of the limiting effect of the size of the renal organ was given by Buse (1971).

A difference in the chemical substances produced by the snails appears to be the most probable way by which *Chaetogaster* could identify the various species. Wright (1959), in a study of the chromatographic pattern of the mucus produced by various species of

Lymnaea, showed that there were species-specific substances in the mucus of the body surface of the snail. He suggested that snails, being non-visual, use chemotactic methods of species recognition. These differences could account for the attraction of the worms to the egg masses and the mucous trail, and possibly to the chemical 'host-factor' emanating from the snails. *Chaetogaster limnaei* from a lake with only one species of snail could not detect the difference between various host species to the same degree as worms from a lake with many. The fact that *C. l. limnaei* from the latter could also detect the difference between *Lymnaea peregra* from various sources indicates a high degree of specificity. Wright (1964) showed chromatographically that there were differences in the mucus of *L. peregra* from various sources: this could explain how detection was achieved.

The occurrence of host-specificity in *Chaetogaster* suggests that the worms might vary on different species of snail. The experiments on the nature of the reaction to the host provided some evidence that the 'preference' was not permanent, but that conditioning was involved. The morphological studies, however, suggested that, where the *Chaetogaster* populations were isolated, physical differences became apparent. It is possible that, just as *C. limnaei* has evolved into the distinct subspecies *C. l. limnaei* and *C. l. vaghini*, so *C. l. limnaei* might evolve into biological races and, eventually, subspecies. As Chandler (1923) pointed out, there are slight physiological contrasts in the different environments of the various hosts and it would therefore be expected that different races of parasite would occur due to the isolation of environments. In the case of *C. l. limnaei*, the isolation on different species of snail could tend to promote the formation of races.

ACKNOWLEDGMENTS

I would like to thank Professor T. B. Reynoldson for his advice and encouragement. This study was carried out during the tenure of an award from the Natural Environment Research Council.

SUMMARY

(1) The differential field distribution of *Chaetogaster limnaei limnaei*, found on the outer surfaces of gastropods, and *C. l. vaghini*, in the renal organ, between two snail species suggested host-specificity.

(2) In twenty localities, *C. l. limnaei* was found in 86% and *C. l. vaghini* in 19% of twenty-one species of gastropod.

(3) Experiments presenting 'choices' between whole snails and between egg masses, mucous trails or 'host-factor' from various species demonstrated a tendency towards host-specificity.

(4) This was more developed in worms from a source with many, rather than a single, gastropod species present: differences could be detected between *Lymnaea peregra* from several sources. Chemical variation in the host mucus might allow this.

(5) The reaction to the host changed after 1 month on a different host species, i.e. conditioning occurred.

(6) Differences in the setal lengths of worms from various localities were apparent.

(7) Specificity might ensure continued attachment to the larger host species: food and living space would then be greater.

(8) Isolation on different snail species could lead to the formation of biological races and eventually subspecies.

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(*Received* 12 *December* 1973)