Maximum local helminth parasite community richness in British freshwater fish: a test of the colonization time hypothesis

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SUMMARY

The investigation of Price & Clancy (1983), which demonstrated a significant positive correlation between total helminth species number per host species and geographical range of freshwater fish host species in Britain, was re-examined using a different measure of parasite species richness. Re-calculation of the correlations between the two parameters after controlling for the effect of the composition of the list of fish by excluding, on biological and distributional grounds, 2 species of agnathans and 7 species of introduced teleosts, and for the effect of sampling effort by using helminth richness in the richest component community of each fish species rather than check-list data, reveals no significant relationship between helminth species richness and host range. Habitat and an omnivorous host diet now appear more significant determinants of helminth richness than the accumulation of parasites by predation. The findings provide little support for the interpretation of the relationship between helminth species richness and host range in terms of island biogeographic theory, but do support an alternative explanation in terms of the colonization time hypothesis, i.e. that helminth species richness is related to the time since the fish host arrived in Britain.

Key words: parasite community, freshwater fish, helminth richness, island biogeography, colonization time hypothesis.

INTRODUCTION

In parallel with the recent upsurge in interest in helminth community ecology, several authors (Kennedy, Bush & Aho, 1986*a*; Aho, Bush & Wolfe, 1991; Bell & Burt, 1991) have attempted to explain the patterns in the number of helminth parasite species in freshwater fish. One of the earliest and most important of such studies was that of Price & Clancy (1983), who examined the relationship between the number of parasite species per host species and host geographic range in respect of freshwater fishes in the British Isles. Using the check-list of Kennedy (1974), they obtained a measure of the species richness per host species, and they used data on host distributions taken from Maitland (1972) to provide a measure of host geographic range, which they then used as an index of host area. The regression of helminth species richness on host geographic range was significant and positive, with range accounting for 68% of the variation in total parasite species number per host species, and host feeding habits for an additional 5%. Introduced species of fish fitted the general pattern seen in the indigenous species and differences in sampling effort appeared unimportant in the light of the strength of the correlation. In the general climate of the time, Price & Clancy (1983) interpreted their species–area relationship in the context of island biogeographic theory (MacArthur & Wilson, 1963, 1967) and the study is generally accepted as an example of the applicability of this theory to host–parasite systems. Several authors publishing around the same time e.g. Dritschilo *et al.* (1975), Kuris & Blaunstein (1977), Kennedy (1978*a*) and Tallamy (1983) also found island biogeographic theory valuable in understanding the ecology of parasite–host systems.

Some of these same authors, however, have expressed reservations about the applicability of island biogeographic theory to parasite–host systems (Kuris & Blaunstein, 1977; Kennedy *et al.* 1986*b*) and indeed the application of the theory has been subject to strong criticism (Birks, 1980; Gilbert, 1980). In the light of these reservations and recent studies relating helminth richness to host range (Gregory, 1990), it would seem particularly appropriate to re-examine the study of Price & Clancy (1983) since it now holds a central position in the field of fish parasite community ecology. In the present study we have re-calculated the correlations between helminth species richness and host geographical area using a different measure of species richness, controlling for the effects of sampling effort, and separating indigenous and introduced fish species. The results are then considered in relation to

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an alternative explanation, namely the colonization time hypothesis (Birks, 1980; Rohde, 1989). The importance of other variables such as host diet as determinants of helminth species richness is also considered and the findings discussed with specific reference to the difficulties resulting from using data derived from check-lists and in using correlations as evidence of causality.

MATERIALS AND METHODS

Data and variables

The list of fish species is based on that of Price & Clancy (1983), but parasite data have not previously been published.

Helminth species richness (*SR*). We have used the total number of helminth species in the richest component community known to the authors as advocated by Kennedy *et al.* (1986*a*). (For further justification, see Discussion section.) For each host species, analyses were performed on: total number of parasitic helminths and total in each of the following parasite taxa: Monogenea, Digenea (adults and larvae), Cestoda (adults and larvae), Nematoda (adults and larvae) and Acanthocephala. A distinction was made between gill parasites (Monogenea) and gut parasites, and between the type of life-cycle (direct versus indirect, and autogenic versus allogenic) (Table 1). Original data sets can be obtained from the authors on request.

Data on host species distribution and biology were taken from Maitland (1972) and Phillips & Rix (1985) (Table 1). Data from 32 fish species were analysed. The 2 agnathans *Lampetra fluviatilis* and *L. planeri* were included by Price & Clancy (1983) and in our initial analysis but were subsequently not considered here since their phylogeny, ecology and diet separate them from all other teleostean fish. (For further justification, see the Results and Discussion sections.) Thirteen predictor variables were tested.

Host range (*HR*). The distributional maps of fish recorded presence or absence of host species in 10 km squares (Maitland, 1972). The number of squares occupied across the British Isles was used as an estimate of geographical distribution, reported as by Price & Clancy (1983).

Number of sympatric fish species a given species can meet in all its communities distributed in the British Isles. This variable was determined by copying each distributional map in Maitland's (1972) key onto a transparency sheet, and superimposing each one onto the 31 other host species distribution maps. Contact dots were recorded as cases of sympatry (noted 1) and then summed, and conversely the absence of contact as an absence of sympatry (noted 0).

Maximal length. This refers to the maximal length (mm) of fish recorded by Maitland (1972). The maximal length describes each host species better than mean length as used by Price & Clancy (1983) since body size appears an integrating factor of species life-cycle.

Weight. Data on the weight of each fish host species are taken from Anonymous (1981). This provides the maximal (record) weight (g) for 24 host species commonly caught in the British Isles.

Host diversity (*HD*). Host diversity refers to the number of species in each family of fish present in the British Isles.

Trophic category (*Tr*). Distributions of species in different categories were mainly carried out following Maitland (1972) who reported the trophic positions of host species in terms of major food types taken by young and adults. Trophic classes identical to those used by Price & Clancy (1983) are as follows: category 1, plants and invertebrates (e.g. roach, minnow); category 2, invertebrates (e.g. three-spined stickleback); category 3, invertebrates and fish (e.g. salmon, trout); category 4, only fish when adult (e.g. pike).

Introduced host species (*Int*). Data obtained from Maitland (1972) and Wheeler (1977) were used to distinguish between non-introduced species (0) and species introduced by man (1).

Relict status of host species (*Relict*). As previously, data from Maitland (1972) and Wheeler (1977) were used to distinguish between non-relict host species (0) and relict species (1).

Length of time a host species has been available for colonization by parasites (*Time*). Data from Wheeler (1977) and Phillips & Rix (1985) were used to distinguish between introduced host species (introduced from *ca.* A.D. 1200 and later) (coded 1), native species present before *ca.* 7500 B.P. and which arrived during land-connections with the continent (coded 2), and relict and migratory euryhaline species, the earliest post-glacial colonizers of the British isles (coded 3). Relict and migratory euryhaline species are separated from native species in this work.

Migration. Fish were coded as non-migrant (0) or migrant (1). Relict species of migratory salmonids which are wholly freshwater in the British isles were considered here as non-migrant.

Eco-ethological guilds (*Eeg*). This refers to a suite of characters including spawning, social and feeding habits (Balon, 1975). Guilds are as follows: guild 1, pelagophils (eel); guild 2, lithophils (e.g. chub, whitefish); guild 3, phytophils (e.g. tench, pike); guild 4, psammophils (gudgeon, stone loach); guild 5, speleophils (bullhead); guild 6, ariadnophils (sticklebacks).

Table 1. Untransformed data for the 32 British freshwater fishes and their helminth parasites

(Variables are as follows: A, area in km²; B, number of sympatric host species; C, maximal length of the host species (mm); D, maximal weight of the host species (g); E, trophic category of host species; F, host diversity; G, introduced host species; H, relict host species; I, time category; J, migratory host species; K, eco-ethological guild category; L, host oxygen tolerance; M, host family category; N, maximum species richness of parasites; O, total Monogenea; P, adult Digenea; Q, larval Digenea; R, adult Cestoda; S, larval Cestoda; T, adult Nematoda; U, larval Nematoda; V, total Acanthocephala; W, total gut parasites; X, autogenic parasites; Y, allogenic parasites.)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
Salmo salar	6070	33	1000	29029	3	4	0	0	3	1	2	1	1	5	0	1	0	1	0	2	0	1	5	5	0
Salmo trutta fario	11800	33	500	8880	3	4	0	0	3	0	2	1	1	16	1	3	1	2	2	3	1	3	11	12	4
Onchorhynchus mykiss	2670	30	450	10965	3	4	1	0	1	0	2	0	1	8	1	1	2	1	2	1	0	0	3	4	4
Salvelinus alpinus	1250	21	400	3373	2	4	0	1	3	0	2	1	1	9	0	2	1	1	1	1	0	3	7	7	2
Coregonus lavaretus	130	14	350		2	2	0	1	3	0	2	1	2	5	1	1	0	1	1	0	0	1	3	4	1
Coregonus albula	250	19	250		2	2	0	1	3	0	2	1	2	4	0	0	1	0	1	0	0	2	2	2	2
Thymallus thymallus	2790	29	400	1899	2	1	0	0	2	0	2	1	3	10	1	2	0	1	2	1	0	3	7	8	2
Esox lucius	8370	33	1000	20581	4	1	0	0	2	0	3	0	4	6	1	0	0	2	0	1	0	2	5	6	0
Cyprinus carpio	4250	31	500	23358	1	16	1	0	1	0	3	0	5	1	2	1	0	1	0	0	0	0	0	0	1
Carassius carassius	1820	29	250	2565	1	16	1	0	1	0	3	0	5	3	1	0	1	1	0	0	0	0	1	2	1
Carassius auratus	290	29	250		1	16	1	0	1	0	3	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Barbus barbus	960	28	500	6520	2	16	0	0	2	0	2	0	5	5	0	1	2	0	0	1	0	1	3	3	2
Gobio gobio	6060	32	150	120	1	16	0	0	2	0	4	1	5	5	1	1	2	0	0	0	0	1	2	3	2
Tinca tinca	5770	31	300	6435	1	16	0	0	2	0	3	0	5	3	1	1	0	0	0	0	0	1	2	3	0
Blicca bjoerkna	790	29	300	425	2	16	0	0	2	0	3	0	5	3	1	0	2	0	0	0	0	0	0	1	2
Abramis brama	6300	32	450	7427	2	16	0	0	2	0	3	0	5	9	3	1	2	1	1	0	0	1	3	6	3
Alburnus alburnus	1650	30	150	120	2	16	0	0	2	0	3	0	5	5	1	1	1	0	0	1	0	1	3	4	1
Phoxinus phoxinus	7670	33	100	23	1	16	0	0	2	0	2	0	5	5	2	1	1	0	0	1	0	0	2	4	1
Scardinius erythrophthalmus	4040	32	300	2041	1	16	0	0	2	0	3	0	5	4	1	0	2	0	0	0	0	1	1	2	2
Rutilus rutilus	8000	33	300	1842	1	16	0	0	2	0	3	0	5	12	5	2	1	2	0	1	0	1	6	11	1
Leuciscus cephalus	4130	31	450	3743	3	16	0	0	2	0	2	0	5	13	4	2	0	3	0	1	0	3	9	13	0
Leuciscus idus	180	29	300	2409	2	16	1	0	1	0	3	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Leuciscus leuciscus	4990	30	250	574	2	16	0	0	2	0	3	0	5	12	3	2	0	3	0	1	0	3	9	12	0
Noemacheilus barbatulus	4710	33	120		2	16	0	0	2	0	4	1	5	4	1	0	0	0	0	0	1	2	0	3	1
Anguilla anguilla	10510	33	1200	5046	3	1	0	0	3	1	1	0	6	9	0	1	1	2	0	3	0	2	6	8	1
Gasterosteus aculeatus	5760	33	60		2	2	0	0	3	1	6	0	7	8	1	2	1	1	2	0	0	1	4	5	3
Pungitius pungitius	1370	31	50		2	2	0	0	2	0	6	0	7	3	0	0	0	1	1	0	0	1	2	2	1
Micropterus salmoides	20	16	350		3	1	1	0	1	0	3	0	8	1	1	0	0	0	0	0	0	0	0	1	0
Perca fluviatilis	8770	33	300	2523	3	3	0	0	2	0	3	0	9	15	1	1	4	2	3	2	1	1	6	7	8
Gymnocephalus cernua	2140	29	180	148	2	3	0	0	2	0	3	0	9	6	0	0	5	0	0	1	0	0	1	1	6
Stizostedion lucioperca	160	25	450	8390	4	3	1	0	1	0	3	0	9	1	0	0	0	0	0	0	0	1	1	1	0
Cottus gobio	4150	31	130	28	2	1	0	0	2	0	3	1	10	6	1	1	3	0	0	0	0	1	2	3	3

Oxygen tolerance. Oxygen tolerance of fish species was coded 1 when fish required well-oxygenated water to survive (e.g. salmon, brown trout) and 0 when fish could thrive in water with low or fluctuating oxygen content (e.g. rainbow trout, carp).

Host family. In order to determine the effect of host family on parasite species richness, 10 host families were coded as follows: (1) Salmonids; (2) Coregonidae; (3) Thymallidae; (4) Esocidae; (5) Cyprinidae; (6) Anguillidae; (7) Gasterosteidae; (8) Centrarchidae; (9) Percidae; (10) Cottidae.

Statistical methods

Standard linear and multiple regression techniques were used. As host range and species richness were not distributed normally these variables were transformed ($\log_e$) to linearize the data (Table 2). The same procedure was applied for each parasite richness by parasite taxa and by type of life-cycle. Both body length and body weight variables were similarly transformed (Eadie, Broekhoven & Colgan, 1987). Eco-ethological guilds and host family qualitative variables were directly replaced by 6 and 10 attributes respectively which each has a value of 0 or 1.

Simple regressions. The search for biological characteristics correlated with species richness was carried out using two regression models. The first consisted of regression of species richness in relation to the 13 explanatory variables listed above, trophic category (*Tr*) and *Time* variables being first coded as linear variables. In the case of *Tr*, this coding makes it possible to test whether there is a positive linear relation between parasite species richness and the position of the host in the food-web and in the case of *Time* variable, between parasite species richness and length of time a host species has been available for parasite colonization. The second model is identical to the first except for the coding of variables *Tr* and *Time*. Firstly, the *Tr* variable was replaced by 4 attributes which each had a value of 0 or 1: *Tr* 1, *Tr* 2, *Tr* 3 and *Tr* 4. These variables are 1, 0, 0 and 0 if the species is a herbivore–detritrivore, 0, 1, 0 and 0 if it is a micro-predator, 0, 0, 1 and 0 if it is an omnivore, 0, 0, 0 and 1 if the species is a top-predator. This transformation permits testing the effect of belonging to a particular trophic category on species richness. Secondly, *Time* variable was replaced by 3 attributes, *Time* 1, *Time* 2 and *Time* 3. Variables *Time* 1, *Time* 2 and *Time* 3 are 1, 0 and 0 if the host species was introduced to the British Isles by man (redundant with *Int* variable), 0, 1 and 0 for native fish species, 0, 0 and 1 for the relict and migratory fish species.

For relationships between quantitative variables, the Bravais-Pearson correlation coefficient was calculated. In the case of relationships between a quantitative variable and a qualitative attribute with two possible values (0 or 1), the point-biserial correlation coefficient was estimated (Dagnélie, 1988).

Multiple regressions. In multiple regression techniques, variables were selected from the result of foreward stepwise regression. At each step, the variable showing the highest partial correlation with the dependent variable was determined and included in the model only if the correlation was significant at the 0·05 level of probability. When a new variable was introduced into the model, the contribution of the previously chosen variables was systematically re-examined and interpreted. The procedure was terminated when no variable could be added to the model. Firstly, the *Time* variable was used as a linear variable, and then replaced by two dummy variables (Draper & Smith, 1966) which are D*Time* 1 and D*Time* 2. Variables are 0, 0 if the species was introduced, 1, 0 if native and 0, 1 if relict/migratory in the British Isles. The dummy variables were included or withdrawn from the model together and their common contributions over and above the possible action of other variables was tested as proposed by Hugueny (1990).

Model quality was determined by studying residuals (observed values minus the values predicted by the regression model). The independence of residual values as a function of species richness value was checked by analysing the sequence of residual signs (Draper & Smith, 1966). Lastly, the quality of the model was evaluated by visual examination of residuals.

Tests of equality between two correlation coefficients were performed with the standard-error method using the inverse tanh transformation, and compared with a theoretical value (Dagnélie, 1988).

RESULTS

Host species, helminth richness and the codings of variables are shown in Table 1. Table 2 summarizes the different relationships between helminth species richness and host range among the 32 host fish species. As revealed by the correlation coefficient, the most significant relationship was obtained following double transformation of the data. This relationship between the transformed variables is also illustrated in Fig. 1. Results also gave satisfactory F-test and Z-linearity test results (Table 2).

Table 3 summarizes the significant (satisfactory F-test) relationships between predictor variables and parasite species richness (total, by parasite taxa and by types of life-cycle). The variable introduced fish species appears to be as equally good a predictor ($r^2 = 0{\cdot}46$, $P < 0{\cdot}0005$) of total helminth richness as host range ($r^2 = 0{\cdot}46$, $P < 0{\cdot}0005$). In other words, the introduced host species variable influences the general host range-total species richness relationship

Table 2. Relationships between helminth species richness (*SR*) per host and host geographical range (*HR*) for the 32 British fish species analysed

(*r*, Correlation coefficient; r^2, determination coefficient; F, F-test, D.F. (1,30), $P < 0{\cdot}0005$; Z, sign test of residuals (best models are indicated by Z statistics in italics, $P < 0{\cdot}01$).)

	Intercept	Slope	*r*	r^2	F	Z
SR/*HR*	2·87	8·22E-4	0·64	0·42	21·38	−0·447
SR/log$_e$*HR*	−6·31	1·63	0·60	0·37	17·26	0·853
Log$_e$*SR*/*HR*	1·23	1·33E-4	0·62	0·38	18·63	*0·196*
Log$_e$*SR*/log$_e$*HR*	−0·62	0·31	0·68	0·46	26·51	*−0·180*

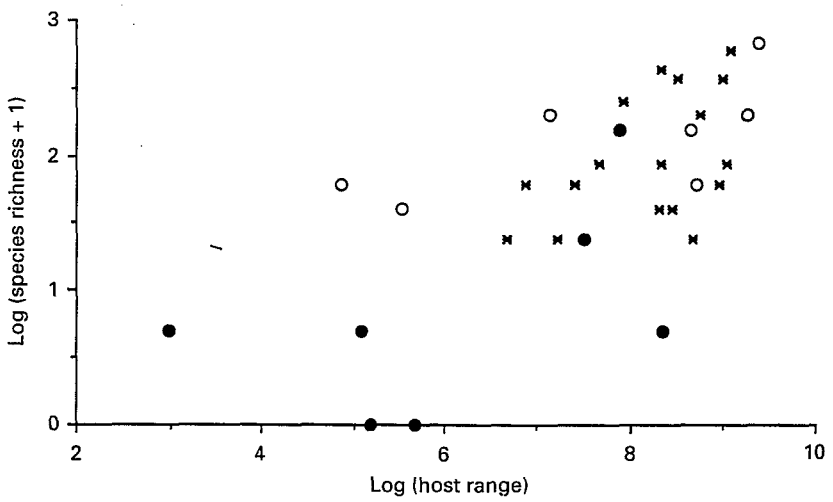

Fig. 1. Relationship between number of helminth species per fish species and host geographical range. Both variables are logarithmically transformed. (●) Introduced species; (✖) native species; (○) relict and migratory species. $y = 0{\cdot}93 + 0{\cdot}16x$, $r^2 = 0{\cdot}46$, $P < 0{\cdot}0005$ (all species); $y = -0{\cdot}33 + 0{\cdot}28x$, $r^2 = 0{\cdot}21$, $P > 0{\cdot}05$ (only native).

Table 3. Correlation coefficient values (*r*) between helminth species richness and some predictor variables used in the analysis for the 32 host species analysed

(Only predictor variables showing a satisfactory F-test result are illustrated here. Total, total species richness; Mon, Monogenea; DiA, adult Digenea; CeA, adult Cestoda; CeL, larval Cestoda; NeA, adult Nematoda; Aca, Acanthocephala; Gut, gut parasites; Aut, autogenic parasites; *Sum*, sum of the distinct parasite richness (by parasite taxa and by types of life-cycle) a given predictor variable can satisfactorily explain. See text for abbreviations of predictor variables. $^1P > 0{\cdot}05$; $^2P < 0{\cdot}025$; $^3P < 0{\cdot}01$; $^4P > 0{\cdot}005$; $^5P < 0{\cdot}001$; $^6P < 0{\cdot}0005$.)

	Species richness									
Predictor variables	Total	Mon	DiA	CeA	CeL	NeA	Aca	Gut	Aut	*Sum*
Log$_e$ *HR*	0·68^6	0·41^2	0·51^3	0·47^3	—	0·49^4	0·35^1	0·53^1	0·59^5	7
Log$_e$ *ML*	—	—	—	—	—	0·46^3	—	—	—	1
HD	—	0·42^2	—	—	−0·53^3	—	—	—	—	2
Int	−0·68^6	—	−0·39^1	—	—	—	−0·62^5	−0·57^5	−0·64^6	4
Time	0·59^5	—	—	0·48^3	—	0·56^5	0·65^6	0·50^3	0·65^6	5
Tr	—	—	—	—	—	−0·42^2	—	—	—	1
*Tr*1	—	—	—	—	−0·37^1	—	−0·37^1	—	—	2
*Tr*3	—	—	—	0·43^2	—	0·60^5	—	—	—	2
*Eeg*1	—	—	—	—	—	0·39^1	—	—	—	1
*Eeg*2	—	—	0·43^2	—	0·37^1	0·40^1	—	0·45^3	0·37^1	5
*Eeg*3	−0·37^1	—	−0·40^1	—	—	—	−0·41^2	−0·39^1	−0·38^1	4
Oxygen tolerance	—	—	—	—	—	—	0·47^3	—	—	1
Salmonids	—	—	0·37^1	—	—	0·48^4	—	0·37^1	—	3
Cyprinids	—	0·44^3	—	—	−0·55^5	—	—	—	—	2
Anguillids	—	—	—	—	—	0·39^1	—	—	—	1

Table 4. Multiple regression analysis of (*a*) $\log_e$ (*parasite species richness*) versus $\log_e$ (*host range*) and *Time* when *Time* variable is considered as a linear variable and (*b*) $\log_e$ (*parasite species richness*) versus $\log_e$ (*host range*) and *Time* when *Time* variable is used with its two dummy variables

(See text for explanations. Abbreviations as in Tables 2 and 3.)

(*a*) Coefficients

$\log_e HR$	*Time*	Intercept	*r*	r^2	F
0·2502 $P < 0·001$	0·4320 $P < 0·001$	−1·0062	0·7862	0·6181	23·50 $P < 0·001$ D.F. (2, 29)

(*b*) Coefficients

$\log_e HR$	D*Time*1	D*Time*2	Intercept	*r*	r^2	F
0·2195 $P < 0·01$	0·6474 $P < 0·001$	0·9114 $P < 0·001$	−0·4718	0·7954	0·6327	16·08 $P < 0·001$ D.F. (3, 28)

Table 5. Correlation coefficient values (*r*) between parasite species richness and some predictor variables used in the analysis for the 25 host species remaining after the withdrawal of the 7 introduced host species

(Only predictor variables showing a satisfactory F-test result are illustrated here. See text and Table 3 for legends and abbreviations. [1] $P < 0·05$; [2] $P < 0·025$; [3] $P < 0·01$; [4] $P < 0·005$; [5] $P < 0·001$; [6] $P < 0·0005$.)

Predictor variables	Species richness												
	Total	Mon	DiA	DiL	CeA	CeL	NeA	NeL	Aca	Gut	Aut	All	*Sum*
$\log_e HR$	0·45[2]	—	—	—	—	—	0·42[1]	—	—	—	0·47[2]	—	2
$\log_e ML$	—	—	—	—	0·41[1]	—	0·56[4]	—	0·44[1]	—	0·41[1]	—	4
HD	—	0·54[4]	—	—	—	−0·55[4]	—	—	—	—	—	—	2
Tr	—	—	—	—	0·58[4]	—	0·54[4]	—	0·40[1]	0·44[1]	—	—	4
*Tr*2	—	—	—	—	—	—	−0·43[1]	—	—	—	—	—	1
*Tr*3	0·52[3]	—	—	—	0·55[4]	—	0·71[6]	0·43[1]	—	0·51[3]	0·50[2]	—	5
Eeg 1	—	—	—	—	—	—	0·40[1]	—	—	—	—	—	1
Eeg 4	—	—	—	—	—	—	—	—	—	−0·40[1]	—	—	1
Salmonids	—	—	—	—	—	—	0·46[2]	—	—	—	—	—	1
Cyprinids	—	0·57[4]	—	—	—	−0·56[4]	—	—	—	—	—	—	2
Anguillids	—	—	—	—	—	—	0·40[1]	—	—	—	—	—	1
Percids	—	—	—	0·57[4]	—	—	—	—	—	—	—	0·59[4]	2

(an effect visible in Fig. 1). Fig. 1 also shows that the regression equation for all species differs from that for native species only, and that the correlation coefficient is not significant when introduced species are removed. There also exists a positive linear relationship between the different fish categories in respect of the time of their presence in the British Isles and the number of parasite species they harbour ($r^2 = 0·36$, $P < 0·001$) (Table 3)

Inclusion of the two species of Agnathans in the analysis gives the following results: $\log_e$ SR/$\log_e$ *HR*, $r = 0·66$, $r^2 = 0·44$ (cf. values for 32 species in Table 2), and again the variable introduced fish species is as good a predictor ($r = 0·59$, $r^2 = 0·35$, $P < 0·5$) as host range. Exclusion of Agnathans, justifiable on biological grounds, does not therefore affect the results significantly.

A multiple regression analysis indicates that the log of host range and *Time* (linear variable) both contribute significantly to the variation of the log of parasite species richness (Table 4*a*). The two predictor variables $\log_e HR$ and *Time* have positive coefficients, which are significantly different from zero in both cases (Table 4*a*). The multiple determination coefficient is high and highly significant ($r^2 = 0·62$, $P < 0·001$). Examination of partial correlation coefficients shows that the *Time* variable is the major variable for explaining the total variation in helminth species richness. These previous results are confirmed by multiple regression calculations using the *Time* variable with its two dummy variables (Table 4*b*).

The withdrawal of the 7 introduced species from simple regression calculations confirms these suggestions (Table 5). Host range no longer behaves as a principal predictor variable of total parasite species richness, and the *Tr* 3 variable is now as good a predictor variable as host range. A diet of inverte-

Table 6. Multiple regressions of parasite species richness (total, by parasite taxa, and by types of life-cycle) versus the main predictor variables retained in the analysis

(Abbreviations are as in Tables 2 and 3.)

	Multiple regression coefficients				
Species richness	1st predictor variable	2nd predictor variable	Intercept	r	F D.F. (2, 22)
Total	*Tr* 3 $P < 0{\cdot}01$	Log_e *HR* $P > 0{\cdot}05$	1·03	0·58	5·73 $P < 0{\cdot}01$
Mon	*HD* $P < 0{\cdot}0005$	Log_e *HR* $P > 0{\cdot}05$	−0·75	0·62	6·83 $P < 0{\cdot}0005$
CeA	*Tr* $P < 0{\cdot}005$	Log_e *HR* $P > 0{\cdot}05$	−1·18	0·63	7·38 $P < 0{\cdot}005$
CeL	*HD* $P < 0{\cdot}01$	*Tr* 4 $P > 0{\cdot}05$	0·71	0·60	6·31 $P < 0{\cdot}01$
NeA	*Tr* 3 $P < 0{\cdot}0005$	Log_e *HR* $P > 0{\cdot}05$	−0·57	0·75	13·80 $P < 0{\cdot}0005$
NeL	*Tr* 3 $P < 0{\cdot}01$	*Eeg* 4 $P > 0{\cdot}05$	—	0·60	6·08 $P < 0{\cdot}01$
Aca	*Tr* $P < 0{\cdot}01$	*Eeg* 3 $P > 0{\cdot}05$	0·49	0·49	3·52 $P < 0{\cdot}05$
Gut	*Tr* 3 $P < 0{\cdot}01$	*Eeg* 4 $P < 0{\cdot}05$	1·35	0·61	6·54 $P < 0{\cdot}01$
Auto	*Tr* 3 $P < 0{\cdot}025$	Log_e *HR* $P > 0{\cdot}05$	0·31	0·58	5·61 $P < 0{\cdot}025$

brates plus fish can now explain total richness equally well, even though no linear relationship was observed between total parasite richness and the position of fish in the food-web. Predictor variables, which previously had their effect masked by the importance of the host range variable, can now be seen to play a stronger role. A comparison between Tables 3 and 5 (by comparison of *Sum* values in each table) shows that the effect of host range (*HR*) decreases considerably as an explanation of the different parasite categories while the effect of maximal length (*ML*) tends to increase, and the effect of *Tr* trophic category linear variable and *Tr* 3 variable now assume greater importance in explaining parasite richness by parasite taxa and types of life-cycle.

Multiple regressions show that host diversity (*HD*) is positively correlated with species richness in Monogenea, and negatively correlated with the number of species of larval Cestoda; that *Tr* (trophic linear variable) explains the richness in both adult Cestoda (equally with *Tr* 3, $u_{obs} = 0{\cdot}146$ and $u_{0{\cdot}560} = 0{\cdot}15$) and Acanthocephala; and that *Tr* 3 (omnivorous category of fish) explains the number of total parasite species, of adult and larval Nematoda, and of gut and autogenic parasites (Table 6). No other predictor variables are significant, except in the case of gut parasites where *Eeg* 4 is the second variable in a stepwise procedure (Table 6). No variable can explain the species richness in adult Digenea (*Tr* is only just not significant), in larval Digena, and in allogenic parasites. Cyprinid fish appear statistically to be strongly parasitized by Monogenea and poorly by larval Cestoda while percid fish are rich in both larval Digenea and allogenic parasites. Anguillid and salmonoid fish appear to be well-parasitized with adult Nematoda.

If the relict fish species (1 Salmonid and 2 Coregonids) are also removed from the calculations, i.e. all species of restricted distribution whether caused by introductions or post-glacial events, this has no significant effect on any of the different regressions. This confirms the earlier findings that correlation coefficients associated with the *Relict* variable were not significant (Tables 3 and 5). Results using multiple regression procedures are identical and confirm that *relict* is not a significant predictor variable.

DISCUSSION

In their original paper, Price & Clancy (1983) found a significant positive correlation between the number of helminth parasite species per host and the geographical range of the host fish species. Their measure of species richness was the total number of helminths reported from each species of fish in the check-list of Kennedy (1974), and they used data from 34 species of British freshwater fish. The inclusion of 2 species of agnathans in our analysis does not affect any of the results or conclusions. Nevertheless, their inclusion would not appear to be justifiable in view of their different phylogeny, ecology and diet and so they were subsequently omitted from the present re-examination. Repeating

the analysis of Price & Clancy (1983) for the remaining 32 species of teleosts gave similar results, with the best correlation being obtained after logarithmic transformation of both species richness and host range variables, and despite controlling for sampling effort by using a different measure of species richness. Such a control is essential (Gregory, 1990), and the measure of species richness adopted here has only minimal dependence on sampling effort. Thus far, therefore, the results of the two investigations are in agreement, and the graphs produced by Price & Clancy (1983) and in this account (Fig. 1) are very similar.

The major area of disagreement comes in relation to the treatment of the introduced fish species. Price & Clancy (1983) noted particularly that introduced species fitted the general pattern seen in the indigenous species, but inspection of our Table 1 suggests that the 7 introduced species are distributed rather differently from the other species. Confirmation of this was sought by determining the correlation for native species only and this was shown to be non-significant. More detailed analysis also indicated that the variable *introduced fish* species was as good a predictor variable of helminth richness as host range. Thus, the introduced species are major determinants of the strong relationship between helminth species richness and host range reported by Price & Clancy (1983). Their interpretation, that introduced species fitted the general pattern, is refuted by the re-analysis presented here, as this indicates that the introduced species are in fact largely responsible for influencing the relationship between the two variables. Correlation in this case is not indicative of causality, and an alternative explanation for the significant correlation when all teleosts are considered, and the lack of significance for native species only must be sought.

The most plausible explanation is that form of the regression between the two parameters visualized in Fig. 1 is being influenced by a third, dependent variable. The most likely identity of this variable is time since the fish species colonized Britain, as this variable is significantly correlated with host range. Introduced species seldom, if ever, bring with them all the parasite species that they harbour in their locality of origin, and of the parasites that they do carry, some will die out in transit, and others will fail to establish in the new locality since suitable intermediate hosts are absent or because the propagule size is too small (Dobson, 1990). Many of the species introduced by man have been transported as eggs, or over long times and distances and so bring no or few parasites with them. Considerations of specificity and ecology suggest that they will require a considerable time to acquire a new helminth fauna derived from the native species of fish, i.e. colonization of a species by parasites takes a finite time. Thus, the parasite fauna of the species introduced into Britain is likely to be far less rich than that of the native species. The native species themselves can be divided into two groups, but both are believed to have colonized Britain a long time before the introduced species (Maitland, 1972; Wheeler, 1977): the relict and migratory species were the earliest colonizers in post-glacial times, and the remaining native species colonized before Britain was separated from continental Europe. Both have therefore had a long time to acquire their helminth fauna, and relict hosts, although limited in distribution, have nevertheless acquired a fauna far richer than that of the introduced species, which have only been in Britain for less than 1000 years. Relict species do not therefore influence the regression in the same way as the introduced species. Confirmation of the importance of colonization time as a determinant variable was obtained from Table 3. The correlation between species richness and time was not significant for native, including relict and migratory species only, but was highly significant for all the 32 fish species when the introduced species were included. The fact that the parasite fauna of relict species is richer than would be predicted by the species richness-area island biogeographic model should in itself cast doubt on the applicability of that model, and indeed other investigations (Kennedy, 1978*b*; Kennedy *et al.* 1986*b*) have shown that island theory is a poor predictor of parasite richness amongst freshwater fish species.

It would appear that the relationship demonstrated by Price & Clancy (1983) and confirmed here was statistically correct, but whereas they interpreted this as evidence of the applicability of island biogeography theory, we suggest that the colonization time hypothesis is a more correct explanation. They did not consider time as a possible variable, but the use of multiple regression techniques in the present study confirms that time has a very strong effect on the correlation. This correlation between time and host range has led to difficulties in the interpretation of other investigations attempting to relate species richness to host area. Several authors have reported relationships between insect species richness and plant area and/or time, but have tended to differ in their interpretation of the relationships. Strong (1974*a*, *b*, 1979) for example favoured an island biogeographical explanation of his data and rejected the time hypothesis, whereas Southwood (1961, 1975) and Moore (1974) have tended to favour time as an explanation of species richness and Birks (1980) specifically drew attention to what he believed was Strong's premature rejection of the time hypothesis. In the case of helminth species richness and fish range, we believe we have provided evidence against the area-richness hypothesis and so we could consider this latter hypothesis to be not only an alternative but also a more satisfactory explanation of the observed relationship.

Recognition of the distinctiveness of the 7 introduced species brings the remaining 25 native species into sharper focus, and permits a search for the identity of the other variables that may influence species richness. It is necessary first, however, to consider the measure of helminth richness employed. Price & Clancy (1983) used Kennedy's (1974) check-list of parasites of British freshwater fish to determine the total number of helminth species known from each fish species in Britain, and this they used as their measure of helminth species richness. There are several objections to this measure. A check-list combines data from different localities and populations obtained at different times, and as such it has no ecological reality. Equally importantly, check-lists of parasites can be biassed by sampling efforts. For example, Gregory (1990) has shown that there is a positive correlation between the number of helminth species per fish and the number of publications cited on the parasites of that fish species, using the check-list of Kennedy (1974). Adopting a completely different approach, Chandler & Cabana (1991) have demonstrated for North American freshwater fish a relationship between parasite richness, dichromatism of the fish and sampling effort. Both studies have shown clearly that the measure of parasite richness may be heavily influenced by sampling effort and that this may in turn lead to incorrect interpretations of species richness–area relationships. The number of parasite species in the richest component community, as used as a measure of species richness in the present study, tends to minimize and control for such differences in sampling effort (Kennedy *et al.* 1986*a*; Kennedy & Bakke, 1989) as it has ecological reality.

Using this different measure of species richness and examining only the native species, explanations of species richness that differ from those proposed by Price & Clancy (1983) become apparent. They believed that geographic range accounted for the largest proportion of the variation in total helminth species number per host, followed by host feeding habits, and they demonstrated that top predators such as *Esox lucius* would support a richer parasite fauna than fish species feeding on algae and invertebrates. By contrast, the present results show that an omnivorous diet of invertebrates and fish can account for much of the variation in total helminth richness of autogenic species per host and of intestinal helminth species per host. Monogenean species richness, on the other hand, is more closely correlated with host diversity as suggested by the studies of Rohde (1989) and Guégan *et al.* (1992). No variable satisfactorily correlated with adult and larval digenean species richness, or with allogenic helminth richness. Host body size is a poor predictor variable, except for Acanthocephala, in contrast to the findings of Bell & Burt (1991), possibly because body size and intestinal length of all fish are poorly correlated. It may be that the greater helminth species richness in predators noted by Price & Clancy (1983) was a reflection of sampling effort and/or the wide range of predators. In the check-list of Kennedy (1974), 37 helminths were recorded from *E. lucius* but the richest component community in pike identified in the present study comprised only 6 species, and the richest helminth component community was recorded in *Salmo trutta*. The results of the present study demonstrate clearly that it is the omnivorous species such as this, *Rutilus rutilus*, *Leuciscus* spp. and *Perca fluviatilis*, that harbour the richer helminth communities. It is likely that this is related to their diet and to habitat, as they are often to be found in productive habitats that harbour a wide range of invertebrate species that can serve as potential intermediate hosts. A very similar explanation was proposed by Aho *et al.* (1991) to account for the species richness of the bowfin *Amia calva*.

By using a different measure of helminth species richness, and at the same time controlling for sampling effort, and by separating indigenous from introduced species, the present study has arrived at very different conclusions from those of Price & Clancy (1983) even though both studies were addressing the same problem. This highlights, particularly, the importance of the methodology adopted in the analysis of helminth community structure and richness, and the inherent problems of interpreting simple correlations. The findings of Price & Clancy (1983) were correct in that the relationship between helminth species richness and host range showed a significant positive correlation. The differences come in interpretation of these data. The employment of multiple regression techniques and the separation for analytical purposes of introduced species led to the recognition of a variable that co-varied with host range, and this variable, time, was shown to have a major influence on species richness and so led to our favouring the time hypothesis rather than the species–area hypothesis as an explanation for the findings. Recognition of the importance of sampling effort as a variable (Gregory, 1990) revealed the extent to which Price & Clancy's (1983) investigation was influenced by this factor, because it was cross-correlated with their measure of species richness. This would seem to be an inevitable consequence of using check-lists as a source of data. At that time, check-lists were often the only source of data and their use undoubtedly advanced our understanding of the factors affecting helminth parasite richness. Nevertheless, we now strongly support the recommendation of Chandler & Cabana (1991) that host–parasite check-lists should not be used as a data source for helminth community investigations or for testing evolutionary hypotheses since they introduce unacceptable levels of bias into the data sets, which may in turn result in statistically correct but biologically misleading interpretations.

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