

Regional versus local helminth parasite richness in British freshwater fish: saturated or unsaturated parasite communities?

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SUMMARY

The relationships between regional species richness and local species richness were examined in respect of helminth parasite communities in 32 species of freshwater fish in the British Isles. Fish were divided into 5 categories, for each of which the goodness of fit of the relationship to linear, exponential and power function models was tested. For all categories of fish combined, there was a significant, positive curvilinear relationship. Nested within this were two other patterns. For introduced fish, a linear model provided the best fit; for euryhaline and relict species it was impossible to determine the best model, but for the other categories the relationship was curvilinear and was best fitted by a power function model. The linear relationship found for introduced fish was interpreted as a temporary situation, reflecting the shortage of time for the communities to become saturated. It corresponded to the linear part of the curvilinear relationship of the other categories, which is believed to represent the fundamental form of the relationship for parasite communities. The communities reached a saturation level of richness, corresponding to the asymptote of the curve, which fell well below regional species richness. Explanations for local saturation are discussed, but neither community structure nor supply-side ecology can yet be preferred. It is concluded that local patterns in helminth community richness, in contrast to those in fish assemblages, are not significantly influenced by patterns on a larger, regional spatial scale and so regional species richness is not a key determinant of local species richness, nor does a knowledge of regional patterns improve predictability of local patterns.

Key words: helminth, community, species richness, saturation, predictability.

INTRODUCTION

One of the principal aims of recent and current investigations into helminth ecology is the recognition of patterns in, and the identification of processes determining, community structure (Esch, Bush & Aho, 1990). Helminth communities in British freshwater fish have been the subject of a number of such studies, partly because the aquatic helminth fauna of the British Isles is comparatively speaking very well known and partly because the area(s) of study are natural, well-defined and with discrete boundaries. Previous investigators have adopted a number of different approaches in their attempts to recognize patterns and predict local helminth richness. Kennedy (1975) attempted to relate parasite community composition to habitat type and later (Kennedy, 1978) attempted to use island biogeographical theory as a basis for prediction of local helminth community richness. Esch *et al.* (1988) focused on colonization patterns of parasites, a theme explored with specific reference to

translocation of hosts by Kennedy, Hartvigsen & Halvorsen (1991). By contrast, Kennedy, Bush & Aho (1986*a*) took a more general approach and compared helminth communities of fish with those of other vertebrate groups. The conclusion of many of these studies and other investigations (Kennedy *et al.* 1986*b*; Kennedy, 1990) was that helminth communities of British freshwater fish were generally species poor and isolationist in nature, and that stochastic processes had played a major part in determining their composition. A very different approach was taken by Price & Clancy (1983): they adopted a regional scale, namely the British Isles, and considered the effects of host range on the number of helminth species harboured by each species of fish. They interpreted their findings as evidence of the applicability of island biogeographical theory, but a subsequent investigation by Guégan & Kennedy (1993), whilst confirming the relationship previously observed on a regional scale, interpreted the findings in terms of the colonization time hypothesis on a regional and local scale. All these investigations have had some measure of success in demonstrating the role of particular factors as determinants of helminth community composition and species richness, but very limited success in

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providing a basis for prediction of local community structure and composition. This lack of success may reflect the facts that helminth communities in British freshwater fish are, for the most part, depauperate and isolationist in nature and that the several factors influencing their composition will vary in importance from locality to locality, i.e. there is multiple causation, or it may reflect the fact that other key factors have not yet been identified or studied.

One factor not yet considered in the context of helminth community richness in British freshwater fish is the relationship between regional helminth richness and local helminth richness. Investigations of this relationship have proved very valuable in assisting understanding of community composition amongst free-living organisms (Ricklefs, 1987; Tonn, 1990): a correlation between species richness at these two levels suggests that processes determining richness at both spatial scales are strongly linked, thus providing a basis for prediction of local richness (Tonn, 1990). The value of changing scales in identifying general mechanisms influencing community structure has become apparent in several recent studies (e.g. Ricklefs, 1987; Rothman & Darling, 1991; Sale & Guy, 1992; Fowler *et al.* 1992; Dayton *et al.* 1992; Levin, 1992; Kennedy & Bush, 1994), and was indeed embedded in the approach of Price & Clancy (1983) although they did not attempt actually to relate regional and local scales. Many studies appear to assume, although this is seldom if ever specifically stated, that regional and local richness are unrelated and independent, yet this can never be totally correct since regional richness must set the boundary to local richness. The only specific investigation of the relationships between regional and local richness of helminth parasite communities was carried out by Aho (1990) on helminths of amphibians and reptiles in North America. Although he considered that regional richness did not contribute significantly to local richness in any of the host taxa he examined, he nevertheless stressed the importance of examining this relationship in other groups of hosts as the precise nature of the relationship could assist understanding of the processes structuring communities.

When analysing the data for their test of the colonization time hypothesis as an explanation for helminth community richness in British freshwater fish Guégan & Kennedy (1993) found clear indications that, as Aho (1990) had advised, an investigation of the relationship between regional and local helminth community richness would reveal patterns that might have predictive value. A preliminary analysis revealed the possible existence of nested subset patterns within the same data set.

This present study therefore presents the results of a detailed analysis of this relationship. Specifically, we aimed to test the hypothesis that local community

richness was dependent on regional community richness. It was not the intention to determine the cause of regional richness, but to examine the form of the relationship between regional and local helminth community richness in the freshwater fishes of the British Isles, and to interpret the findings in relation to the processes determining the helminth community richness that we observed.

MATERIALS AND METHODS

Data and variables

The investigation was restricted to the helminth fauna of the freshwater and migratory fish of the British Isles. This geographical unit, with its finite boundaries, was considered to be the region for the present study. The list of fish species studied is given in Table 1: this is the same list as that used by Guégan & Kennedy (1993), and reasons for the exclusion of some species, and particularly agnathans from the list used by Price & Clancy (1983), are given by Guégan & Kennedy (1993). Regional helminth species richness is taken to be the total number of helminth species reported from each of the species of fish under consideration, and is based on the check list of Kennedy (1974) as updated in Guégan & Kennedy (1993). For each fish species, this represents the regional pool from which all local pools are drawn and so sets the limit to richness of any local pool. The measure of local helminth species richness adopted was the total number of helminth species in the richest component community known to the authors (for justification and further explanation see Guégan & Kennedy (1993)). Data on host range were obtained from Price & Clancy (1983), and the number of parasite communities analysed for each species of fish (compiled from the literature and unpublished information) was adopted as a measure of sampling effort. Fish were divided into the same categories as those used by Guégan & Kennedy (1993) based on the length of time a host species has been available for colonization by parasites in the British Isles, namely; relict and migratory euryhaline species (RE), introduced species (I) and native species (N).

Statistical methods

Standard linear regression techniques, correlation coefficients and ANOVA were employed (Dagnélie, 1988; Sokal & Rolf, 1981). Relationships between regional and local helminth species richness were determined for all species of fish, and separately for the categories of introduced species, native species only, euryhaline and relict fish, and cyprinids (the largest single family). Salmonids, coregonids and percids were also considered for separate analysis,

Table 1. Untransformed data for the 32 British freshwater fishes, their regional parasite richness (*RSR*), their local parasite richness (*LSR*), their host range (*HR*), the sampling effort as expressed by the number of parasite communities analysed (*SE*), and the Fish category as the length of time a host species has been available for colonization by parasites (*FC*)

(RE = relict euryhaline; N = native; I = introduced.)

| Fish species | Variables | | | | |
|------------------------------------|-----------------|------------|--------------------|-----------|-----------|
| | <i>RSR</i> | <i>LSR</i> | <i>HR</i> | <i>SE</i> | <i>FC</i> |
| <i>Salmo salar</i> | 26 | 5 | 6070 ⁵ | 10 | RE |
| <i>Salmo trutta fario</i> | 47 ^r | 16 | 11800 ¹ | 15 | RE |
| <i>Oncorhynchus mykiss</i> | 17 | 8 | 2670 ¹ | 6 | I |
| <i>Salvelinus alpinus</i> | 11 | 9 | 1250 ² | 9 | RE |
| <i>Coregonus lavaretus</i> | 10 | 5 | 130 ³ | 3 | RE |
| <i>Coregonus albula</i> * | 4 | 4 | 250 ² | 3 | RE |
| <i>Thymallus thymallus</i> | 19 | 10 | 2790 ¹ | 10 | N |
| <i>Esox lucius</i> | 37 ^r | 6 | 8370 ⁴ | 12 | N |
| <i>Cyprinus carpio</i> | 3 ^r | 2 | 4250 ¹ | 3 | I |
| <i>Carassius carassius</i> | 7 | 3 | 1820 ¹ | 4 | I |
| <i>Carassius auratus</i> | 0 ^r | 0 | 290 ² | 2 | I |
| <i>Barbus barbus</i> * | 5 | 5 | 960 ¹ | 2 | N |
| <i>Gobio gobio</i> | 10 | 5 | 6060 ¹ | 6 | N |
| <i>Tinca tinca</i> | 4 | 3 | 5770 ¹⁰ | 7 | N |
| <i>Blicca bjoerkna</i> | 4 | 3 | 790 ⁶ | 4 | N |
| <i>Abramis brama</i> | 19 | 9 | 6300 ⁷ | 11 | N |
| <i>Alburnus alburnus</i> * | 5 | 5 | 1650 ² | 4 | N |
| <i>Phoxinus phoxinus</i> | 26 | 5 | 7670 ⁶ | 5 | N |
| <i>Scardinius erythrophthalmus</i> | 12 | 4 | 4040 ⁷ | 4 | N |
| <i>Rutilus rutilus</i> | 34 ^r | 12 | 8000 ⁵ | 18 | N |
| <i>Leuciscus cephalus</i> | 21 | 13 | 4130 ¹⁶ | 8 | N |
| <i>Leuciscus idus</i> | 0 ^r | 0 | 180 ² | 3 | I |
| <i>Leuciscus leuciscus</i> | 25 | 12 | 4990 ¹⁷ | 8 | N |
| <i>Noemacheilus barbatulus</i> | 6 | 4 | 4710 ¹³ | 3 | N |
| <i>Anguilla anguilla</i> | 20 | 9 | 10510 ² | 15 | RE |
| <i>Gasterosteus aculeatus</i> | 27 | 8 | 5760 ¹¹ | 11 | RE |
| <i>Pungitius pungitius</i> | 5 | 3 | 1370 ³ | 3 | N |
| <i>Micropterus salmoides</i> | 1 ^r | 1 | 20 ³ | 2 | I |
| <i>Perca fluviatilis</i> | 34 ^r | 5 | 8770 ² | 24 | N |
| <i>Gymnocephalus cernua</i> | 13 | 6 | 2140 ² | 7 | N |
| <i>Stizostedion lucioperca</i> | 1 ^r | 1 | 160 ³ | 2 | I |
| <i>Cottus gobio</i> | 6 | 6 | 4150 ¹⁵ | 4 | N |

* Species richness values have been here corrected in accordance with new values obtained on local species richness presented by Guégan & Kennedy (1993).

but in each group the number of species was too small to warrant it. In view of the comments of Gregory (1990), the possible effects of other correlated determinant variables such as sampling effort and host range were examined and where necessary controlled for in regression models. The analyses thus utilized partial correlation coefficients to estimate the correlations between pairs of variables when the effects of other specified variables are held constant (Sokal & Rolf, 1981). As sampling effort and host range were not distributed normally, these variables were transformed (\log_e) to linearize the data.

To test the shape of a relationship, we proceeded as follows. Untransformed, exponential and power function models were fitted to the relationship for

each category of fish. The model that adequately linearized the relationship and reduced the variation of points around the regression line was accepted as the best model (Connor & McCoy, 1979). This was confirmed by visual inspection of graphical plots of each data set for the untransformed and for all transformed models. If neither the untransformed nor the transformed models linearized the relationship, no best model was designated. If two or more models linearized the relationship and reduced scatter, the model with both highest r and F-test values was accepted as best. Linearity test values were used as additional, subsequent measures to confirm or refute previous conclusions.

Model quality was determined by studying residuals (observed values minus the values predicted by

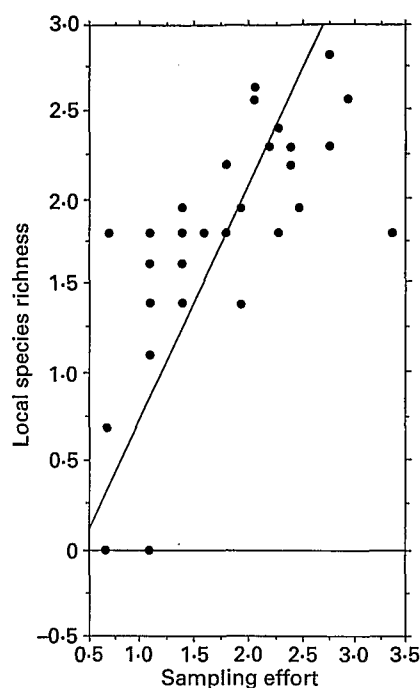


Fig. 1. Relationship between local helminth species richness and sampling effort measured as the number of component communities examined per fish species (after double logarithmic transformation) across 32 fish species in the British Isles ($r = 0.709$, $P < 0.0001$, $y = 0.740x + 0.443$).

the regression model) and was then or finally evaluated by visual examination of residuals.

RESULTS

Untransformed data for the 32 species of freshwater fish showing regional helminth species richness (RSR), maximal local helminth species richness (LSR), host range (HR), sampling effort (SE) and fish category (FC) are presented in Table 1. Regression relationships between RSR and LSR for the five categories of host are given in Tables 2–6, and illustrated in Figs 2–6. We attach particular importance to the shape of the relationships between the two variables (Figures) as well as to the strength

Table 2B. Partial correlation coefficients between regional helminth parasite species richness (RSR) per host species and local helminth parasite species richness (LSR) for 7 British introduced fish species analysed after controlling for the effect of specified variables

(r , Correlation coefficient; r_{partial} , partial correlation coefficient after control by a third variable, see text for more explanations.)

| Controlled variable | r No | r_{partial} Sampling effort | r_{partial} Host range |
|---------------------|-----------|---|------------------------------------|
| $RSR-LSR$ | 0.993 | 0.991 $P = 0.0001$ | 0.992 $P = 0.0001$ |

of the relationships (Tables). If the relationship is linear with a slope greater than zero, it suggests that LSR is very dependent on RSR ; if the relationship is linear but with a slope of zero, it suggests independence between the variables; if the relationship is curvilinear, it suggests an increasing measure of independence resulting in local community saturation.

When the relationship between LSR and SE is considered for all fish species (Fig. 1), it is clear that there is a significant, positive, linear relationship between these two variables. In view of this finding, relationships between RSR and LSR were examined in two stages: initially, correlation coefficients were determined e.g. Table 2A, and then the relationship was re-examined using partial correlation coefficients to control for SE and, as a precaution, for HR , e.g. Table 2B. The $LSR-HR$ relationship is not figured as it shows an identical pattern.

Two patterns of relationship between RSR and LSR are apparent in the data set. In the cases of introduced fish and euryhaline/relict fish, a linear model of the form $y = ax + b$ (where a and b are constants) appears to provide a better fit to the data (Figs 2 and 3). In the cases of the other three categories of fish, namely all fish species, native fish and cyprinids respectively, a power function of the

Table 2A. Relationships between regional helminth parasite species richness (RSR) per host species and local helminth parasite species richness (LSR) for 7 British introduced fish species analysed

(r , Correlation coefficient; r^2 , determination coefficient; F, F-test, D.F. (1, 5); linearity test (best models are indicated by statistics in italics).)

| | r | r^2 | Intercept | Slope | F-test | P | Linearity test |
|-------------------------------|-------|-------|-----------|-------|---------|--------|----------------|
| $RSR-LSR$ | 0.993 | 0.987 | 0.281 | 0.449 | 367.347 | 0.0001 | <i>1.046</i> |
| $RSR-\log_e(1+LSR)$ | 0.919 | 0.845 | 0.385 | 0.116 | 27.342 | 0.0034 | <i>0.972</i> |
| $\log_e(1+RSR)-LSR$ | 0.935 | 0.874 | -0.533 | 2.419 | 34.713 | 0.0020 | 10.616 |
| $\log_e(1+RSR)-\log_e(1+LSR)$ | 0.990 | 0.979 | 0.076 | 0.715 | 234.868 | 0.0001 | <i>0.093</i> |

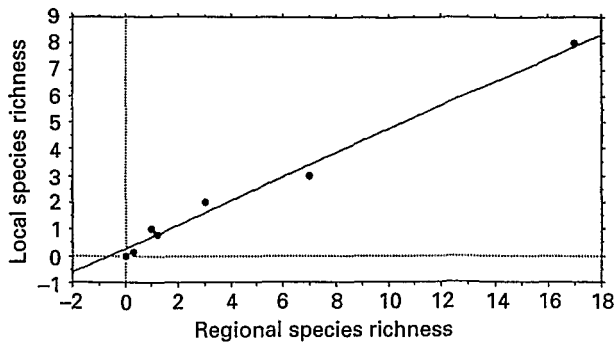


Fig. 2. Relationship between number of regional helminth species (*RSR*) and local helminth species (*LSR*) per introduced fish species (7 species) in the British Isles ($y = 0.449x + 0.281$, $P < 0.0001$).

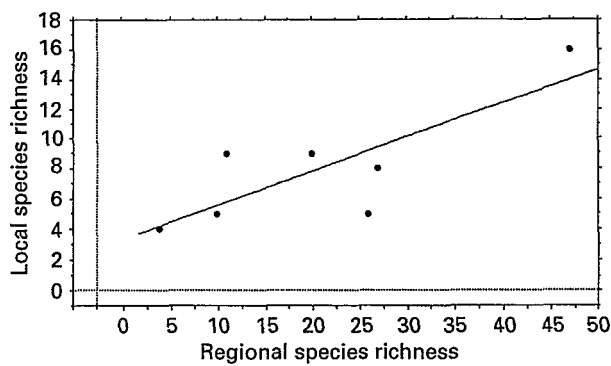


Fig. 3. Relationship between number of regional helminth species (*RSR*) and local helminth species (*LSR*) per euryhaline (migratory) plus relict fish species (7 species) in the British Isles. $y = 0.0227x + 3.301$, $P < 0.303$. After controlling for sampling effort and host range, the relationship is not significant.

form $y = dx^c$ (where c and d are constants) provides the better fit (Figs 4, 5 and 6). The same two patterns are apparent when the regression relationships are considered in detail: in the case of introduced fish (Table 2) and euryhaline/relict fish (Table 3) the

Table 3B. Partial correlation coefficients between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 7 euryhaline and relict British fish species analysed after controlling for the effect of specified variables

(r , Correlation coefficient; r_{partial} , partial correlation coefficient after control by a third variable, see text for more explanations.)

| Controlled variable | r No | r_{partial} Sampling effort | r_{partial} Host range |
|---------------------|-----------|---|------------------------------------|
| <i>RSR-LSR</i> | 0.801 | 0.579 $P = 0.1250$ | 0.634 $P = 0.0870$ |

highest values of the correlation coefficient were obtained for the simple linear relationship of *RSR-LSR*, whereas in the cases of the other three categories (Tables 4, 5 and 6) the highest values of the correlation coefficient were obtained after double logarithmic transformation of the variables, i.e. a power function provides the best regression model.

Detailed analyses of the relationships between *RSR* and *LSR* for introduced fish are shown in Table 2 and Fig. 2. The highest values of r were obtained for the linear model and for the double logarithmic transformation of the data (Table 2A). Both gave satisfactory linearity test values. However, the fact that the highest values of r , r^2 and the F-test were all obtained for the simple linear relationship of *RSR-LSR* and that this relationship is highly significant is taken to mean that the linear model provides the best fit for the relationship. Even after controlling for the effects of host range and sampling effort, the relationship remains highly significant (Table 2B).

In the case of euryhaline and relict fish, the highest values of r and r^2 are again obtained for the simple linear model of *RSR-LSR* and this model also

Table 3A. Relationships between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 7 euryhaline and relict British fish species analysed

(r , Correlation coefficient; r^2 , determination coefficient; F, F-test, D.F. (1, 5); linearity test (best models are indicated by statistics in italics).)

| | r | r^2 | Intercept | Slope | F-test | P | Linearity test |
|--|-------|-------|-----------|-------|--------|--------|----------------|
| <i>RSR-LSR</i> | 0.801 | 0.642 | 3.301 | 0.227 | 8.968 | 0.0303 | 63.190 |
| <i>RSR-log_e(1+LSR)</i> | 0.761 | 0.579 | 1.659 | 0.022 | 6.886 | 0.0469 | <i>0.827</i> |
| <i>log_e(1+RSR)-LSR</i> | 0.705 | 0.497 | -2.967 | 3.832 | 4.947 | 0.0767 | 102.407 |
| <i>log_e(1+RSR)-log_e(1+LSR)</i> | 0.724 | 0.524 | 0.961 | 0.404 | 5.503 | 0.0659 | <i>0.962</i> |

Table 4A. Relationships between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 32 British fish species analysed

(*r*, Correlation coefficient; *r*², determination coefficient; *F*, *F*-test, D.F. (1, 30); linearity test (best model is indicated by statistics in italics).)

| | <i>r</i> | <i>r</i> ² | Intercept | Slope | <i>F</i> -test | <i>P</i> | Linearity test |
|---|----------|-----------------------|-----------|-------|----------------|----------|----------------|
| <i>RSR</i> - <i>LSR</i> | 0.750 | 0.563 | 2.480 | 0.235 | 38.673 | 0.0001 | 421.368 |
| <i>RSR</i> -log _e (1 + <i>LSR</i>) | 0.705 | 0.497 | 1.177 | 0.039 | 29.668 | 0.0001 | 16.473 |
| log _e (1 + <i>RSR</i>)- <i>LSR</i> | 0.792 | 0.628 | -1.032 | 2.963 | 50.564 | 0.0001 | 330.890 |
| log _e (1 + <i>RSR</i>)-log _e (1 + <i>LSR</i>) | 0.892 | 0.795 | 0.367 | 0.590 | 116.368 | 0.0001 | <i>6.003</i> |

Table 4B. Partial correlation coefficients between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 32 British fish species analysed after controlling for the effect of specified variables

(*r*, Correlation coefficient; *r*_{partial}, partial correlation coefficient after control by a third variable, see text for more explanations.)

| Controlled variable | <i>r</i> No | <i>r</i> _{partial} Sampling effort | <i>r</i> _{partial} Host range |
|---|----------------|---|--|
| log _e (1 + <i>RSR</i>)-log _e (1 + <i>LSR</i>) | 0.892 | 0.773 <i>P</i> = 0.0001 | 0.797 <i>P</i> = 0.0001 |

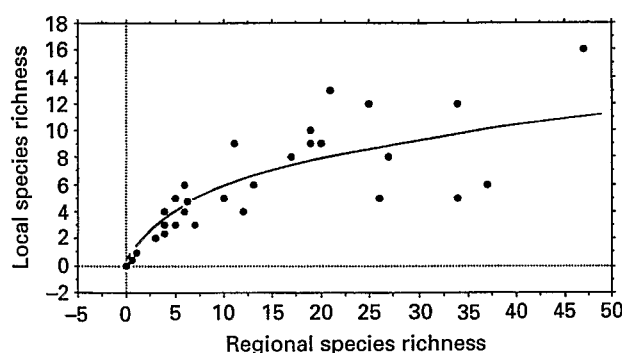


Fig. 4. Relationship between number of regional helminth species (*RSR*) and local helminth species (*LSR*) per each total fish species (32 species) in the British Isles. $y = \text{Exp}^{0.367 * x^{0.590}}$, $P < 0.0001$.

provides the best *F*-test results (Table 3A). The most significant results of the linearity tests, however, indicate that a semi-logarithmic model and the power model provide the best fits to the data. The form of the relationship is thus not so clear for this category of host, and indeed after controlling for the effects of *SE* and *HR* (Table 3B) the relationship is no longer significant and there is no evidence to suggest that it is either linear or curvilinear. It is thus impossible to determine which model provides the

best fit, and the line drawn in Fig. 3 is for a linear model and for illustrative purposes only.

When all fish species are considered together (Table 4 and Fig. 4) it is clear that the highest values of *r*, *r*² and the *F*-test are obtained following double logarithmic transformation of the data. The relationship is significant, and provides a satisfactory value for the linearity test (Table 4A). Even after controlling for *SE* and *HR*, the relationship remains highly significant (Table 4B). It can therefore be concluded that for this category of fish the best model is a power function, described by the parameters illustrated in Fig. 4.

In the cases of native fish species (Table 5) and cyprinids only (Table 6) it is again clear that power functions provide the best models. For both categories of fish, highest values of *r*, *r*² and the *F*-test are obtained following double logarithmic transformation of the data. These values are significant and provide satisfactory values for the linearity tests (Tables 5A and 6A). The relationships remain highly significant even after controlling for *SE* and *HR* (Tables 5B and 6B). It can thus be concluded that for these categories of fish the best models are power functions, and that the relationships are curvilinear (Figs 5 and 6).

Table 5A. Relationships between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 18 native British fish species analysed

(*r*, Correlation coefficient; *r*², determination coefficient; F, F-test, D.F. (1, 14); linearity test (best models are indicated by statistics in italics).)

| | <i>r</i> | <i>r</i> ² | Intercept | Slope | F-test | <i>P</i> | Linearity test |
|--|----------|-----------------------|-----------|-------|--------|----------|----------------|
| <i>RSR-LSR</i> | 0.553 | 0.306 | 3.937 | 0.158 | 7.051 | 0.0173 | 178.775 |
| <i>RSR-log_e(1 + LSR)</i> | 0.588 | 0.345 | 1.591 | 0.021 | 8.444 | 0.0103 | 2.822 |
| <i>log_e(1 + RSR)-LSR</i> | 0.634 | 0.402 | -0.846 | 2.824 | 10.738 | 0.0047 | 157.312 |
| <i>log_e(1 + RSR)-log_e(1 + LSR)</i> | 0.678 | 0.459 | 0.949 | 0.378 | 13.585 | 0.0020 | 2.375 |

Table 5B. Partial correlation coefficients between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 18 native British fish species analysed after after controlling for the effect of specified variables

(*r*, Correlation coefficient; *r*_{partial}, partial correlation coefficient after control by a third variable, see text for more explanations.)

| Controlled variable | <i>r</i> No | <i>r</i> _{partial} Sampling effort | <i>r</i> _{partial} Host range |
|--|----------------|---|---|
| <i>log_e(1 + RSR)-log_e(1 + LSR)</i> | 0.678 | 0.508 <i>P</i> = 0.005 | 0.641 <i>P</i> = 0.001 |

Table 6A. Relationships between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 16 Cyprinid British fish species analysed

(*r*, Correlation coefficient; *r*², determination coefficient; F, F-test, D.F. (1, 14); linearity test (best model is indicated by statistics in italics).)

| | <i>r</i> | <i>r</i> ² | Intercept | Slope | F-test | <i>P</i> | Linearity test |
|--|----------|-----------------------|-----------|-------|---------|----------|----------------|
| <i>RSR-LSR</i> | 0.852 | 0.726 | 1.544 | 0.333 | 37.042 | 0.0001 | 159.451 |
| <i>RSR-log_e(1 + LSR)</i> | 0.781 | 0.610 | 0.948 | 0.058 | 21.861 | 0.0004 | 9.345 |
| <i>log_e(1 + RSR)-LSR</i> | 0.840 | 0.706 | -1.400 | 3.218 | 33.595 | 0.0001 | 102.730 |
| <i>log_e(1 + RSR)-log_e(1 + LSR)</i> | 0.937 | 0.878 | 0.178 | 0.685 | 100.360 | 0.0001 | 2.425 |

Table 6B. Partial correlation coefficients between regional helminth parasite species richness (*RSR*) per host species and local helminth parasite species richness (*LSR*) in maximum component communities for 16 Cyprinid British fish species analysed after controlling for the effect of specified variables

(*r*, Correlation coefficient; *r*_{partial}, partial correlation coefficient after control by a third variable, see text for more explanations.)

| Controlled variable | <i>r</i> No | <i>r</i> _{partial} Sampling effort | <i>r</i> _{partial} Host range |
|--|----------------|---|---|
| <i>log_e(1 + RSR)-log_e(1 + LSR)</i> | 0.937 | 0.864 <i>P</i> = 0.0001 | 0.835 <i>P</i> = 0.0001 |

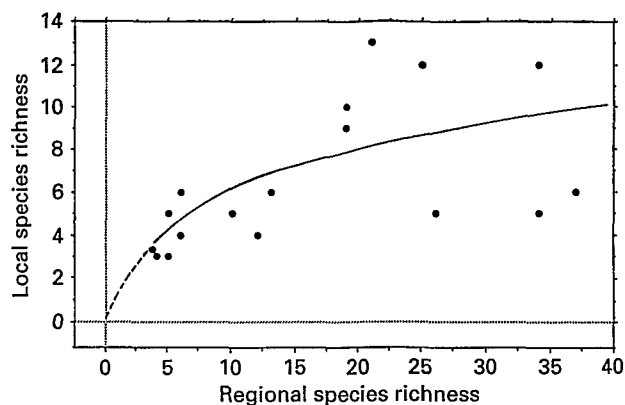


Fig. 5. Relationship between number of regional helminth species (RSR) and local helminth species (LSR) per native fish species (18 species) in the British Isles. $y = \text{Exp}^{0.949 * x^{0.378}}$, $P < 0.0020$.

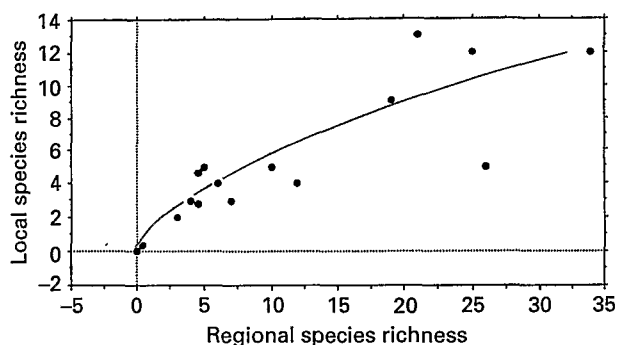


Fig. 6. Relationship between number of regional helminth species (RSR) and local helminth species (LSR) per Cyprinid fish species (16 species) in the British Isles. $y = \text{Exp}^{0.178 * x^{0.685}}$, $P < 0.0001$.

DISCUSSION

Previous studies on helminth communities of British freshwater fish have, with the notable exceptions of Price & Clancy (1983) and Guégan & Kennedy (1993), tended to focus on local community richness and have been conducted at the local level, e.g. Esch *et al.* (1988) and Kennedy (1990, 1993*a, b*). The importance of changing the scale of an investigation to a regional one lies in the fact that processes operating on the larger scale may determine what happens at the smaller scale (Tonn, 1990; Levin, 1992; Sale & Guy, 1992). It is also on occasion easier to detect patterns on a larger scale, since these may be obscured on the local scale by extensive local variation and noise in the system (Sale & Guy, 1992; Kennedy & Bush, 1994). Both Price & Clancy (1983) and Guégan & Kennedy (1993) have identified a pattern at the regional scale, even if they differ in its interpretation, and so the principal objective of this investigation was to determine whether regional processes did affect local ones, and if so to what extent.

When the correlations between RSR and LSR were examined, it became evident that for all

categories of fish there existed a significant, positive relationship between the two variables. Nested within the data set, however, two other patterns emerged. For three categories of fish, namely total fish, native fish and cyprinids, the relationship was curvilinear and best described by a power function model. This relationship was unchanged and remained significant even after controlling for SE and HR , as recommended by Gregory (1990). The three graphs illustrating the relationship were very similar in shape and in the highest value of LSR . This is not surprising, in that the three categories are not independent of each other and each is to a considerable extent a subset of the other. The differences in LSR between fish species have been considered in an earlier study (Guégan & Kennedy, 1993) and so will not be discussed further. In contrast to these findings, the relationship between RSR and LSR for introduced fish was clearly linear and best described by a linear model. For the category of euryhaline and relict fish, it proved impossible to recognize which model provided the best fit.

Turning first to this category of euryhaline and relict fish, inspection of Fig. 3 suggests that the relationship is heavily influenced by the values for *Salmo trutta* (the isolated point with maximum LSR and RSR values in Fig. 3). Re-calculation of the correlation coefficient for the linear model omitting values for *S. trutta* gives results of $r = 0.356$, $r^2 = 0.127$ and $P = 0.488$ (N.S.), thus confirming the weakness of the relationship. There appear to be three possible explanations for the form of the relationship observed and the lack of significance in the data. (1) This could be considered an artificial grouping, in that the two categories may be unrelated and have different distribution patterns with euryhaline species having a wide HR and relict species a narrow one. (2) The lack of significance is a reflection of the small number (7) of species studied. However, the category of introduced fish also comprised 7 species, yet produced significant results. (3) The other dependent variables SR and HR exerted an excessive influence in this category of fish. In support of this explanation is the fact that the relationship appeared significant until the effects of the other variables were taken into account, and it is evident from Table 1 that there has been a very low sampling effort on many of the relict species. Any one or combination of these explanations may apply. It is clear from Table 1 that relict species (*Coregonus* spp.) do all have a low HR and SE , although this is increasingly less true of *Salvelinus alpinus* and *Salmo* spp., and these two variables do influence the regression severely. Relict species also differ in having low LSR and RSR values, whereas values of these two variables for euryhaline fish are much higher. It is suggested therefore that the lack of a clear relationship between regional and local richness in this group reflects its bimodal composition, in

that it comprises one group of fish with a wide range and rich helminth communities that have been subject to several studies and another group of restricted range which have poor communities and have been subject to low sampling effort.

The linear relationship between *RSR* and *LSR* for introduced fish is a much stronger one than that for euryhaline and relict fish. Re-calculation of the relationship omitting values for *Oncorhynchus mykiss* (the isolated point with maximum values in Fig. 2) does not affect the relationship or its significance (new values of $r = 0.956$, $r^2 = 0.915$, $P = 0.003$). However, it must be interpreted in association with the low levels of species richness evident in fish in this category. The maximum value of *LSR* was 8, compared to an overall maximum of 17, but in all the other species in this category values of *LSR* fell below 3. Thus, helminth communities in this category are for the most part species poor. This is believed to reflect the short time since their arrival in Britain (Guégan & Kennedy, 1993). When introduced to Britain, such fish are either parasite free or contain only a very few native species (Kennedy, 1993a) and it is believed that they are still in the process of acquiring species from native fish, and that they will successively accumulate more parasite species over time (Guégan & Kennedy, 1993). It seems likely that the linear relationship in this category reflects the unsaturated nature of the helminth communities, and corresponds to the linear part of the curvilinear relationship evident in the other categories of fish. It can be predicted that as they acquire more parasite species, the relationship will become curvilinear.

If this explanation and prediction is accepted, then it can be deduced that the fundamental relationship between *RSR* and *LSR* is curvilinear in form: introduced fish are *sensu stricto* a temporary exception, and euryhaline and relict fish an artifactual exception. It can thus be concluded that these two variables are correlated, as predicted, and so the hypothesis that *LSR* is related to *RSR* is not refuted. This is not an unexpected conclusion, since the two variables are not ultimately independent in that *RSR* sets the boundary to *LSR* as the richest possible *LSR* cannot exceed *RSR*. In fact, in the majority of fish species, and especially when values of both variables are high, *LSR* is considerably lower than *RSR*. For example, in the richest species of fish *Salmo trutta* the richest *LSR* of 16 falls well below the value of 47 for *RSR*. *LSR* only approached or equalled *RSR* in the few species in which values of both variables were low, and when *SE* was low, and this is probably a reflection of unsaturated communities in the case of introduced fish and/or low sampling effort leading to a low estimate of *RSR*: this is essentially the sum of all *LSRs*.

It is therefore not the fact that the two variables are correlated that is the most interesting finding: it

is rather the shape of the relationship. The key questions are therefore: why *LSR* does not continue to increase with *RSR*; why there is an increasing degree of independence between the two variables; and what actually sets the maximum limit to *LSR*. The curvilinear form of the relationship suggests strongly that local helminth communities become saturated with species and that richness does not exceed a maximum value, the asymptote of the curve, which falls well below *RSR*.

There are two fundamentally different classes of explanation for such local saturation of a helminth community. The first interprets saturation as being a consequence of the community structure itself. When a community is species poor, there are vacant niches available and the community is easily invadible by newly acquired species. This is the situation with introduced hosts, where the helminth communities are still unsaturated, and may be the situation for native fish species on remote islands (Kennedy *et al.* 1986b). However, as the helminth communities become richer, there are fewer vacant niches, they are less easily invadible, they are more likely to be species packed and so inter-specific competition is more likely to occur between species and become important in structuring communities. The communities have in essence changed from isolationist to interactive in nature and become more similar to helminth communities in aquatic birds (Bush, 1990). On this explanation, the limit to the richness of any local helminth community is set by available niche space and inter-specific interactions. There is some evidence that this explanation may be the most plausible for helminth communities in *Anguilla anguilla*, and especially for the acanthocephalan component, since studies by Kennedy (1990, 1993b) have indicated that there may be a fixed number of niches available and there is clear evidence of competition between some species of helminth resulting in the exclusion of species from a community (Bates & Kennedy, 1990; Kennedy, 1992). Although a curvilinear relationship is by itself weak evidence for interspecific interactions between helminth species, it is certainly consistent with such interactions occurring.

The alternative explanation is that *RSR* is not in fact the real or best measure of the pool of helminth species available to a fish species in any locality. Although it sets the absolute boundary to *LSR*, it is in fact highly improbable, if not impossible, that all the helminth species present in a region could ever be present in any single locality. The component community in any locality is dependent on chance introduction events, on the presence and abundance of the correct host species and through them on the correct physico-chemical and biotic characteristics of the locality, and on the survival of the colonizing propagule: introductions are far commoner than successful colonizations (Kennedy, 1993a). The

helminth species pool in any locality will thus be finite and far lower than the regional pool of which it is a nested subset. Most parasite species are in fact not cosmopolitan or regular in distribution, but very local and patchy reflecting local conditions (Price, 1980). In any locality, the component community is in effect a subset of the compound community (Kennedy, 1990) and this is in reality the pool from which the component community is drawn (see Neraasen & Holmes, 1975). Thus, local saturation of the helminth community reflects saturation of the compound community and the locality itself. This is effectively a supply-side situation, and there will be considerable variation between localities in their saturation levels reflecting their different conditions and histories. The community of helminths in each locality is a consequence of chance, stochastic events and so is stochastic rather than deterministic in composition. Support for this view of helminth communities comes from the studies of Kennedy *et al.* (1986), Esch *et al.* (1988), Kennedy (1990) and Aho (1990).

It is not really possible in the present state of knowledge to favour either explanation and indeed they may not be exclusive, as Holmes (1986) has argued persuasively for pluralistic explanations and an acceptance of multiple causality. In the only directly comparable parasitological study to this, Aho (1990) investigated the relationship between *RSR* and *LSR* for helminths of amphibians and reptiles in North America. He used slightly different methodology, grouped his hosts by taxa not biology or history, and made no attempt to determine the exact form of the relationships of the best fit models, but his conclusions were essentially similar to ours. In only one host did *LSR* change significantly with *RSR*: in all other hosts he found no significant changes in local richness with increasing regional richness and so he concluded that *RSR* did not make a strong contribution to *LSR* in the species he examined. He believed that the communities he studied were species poor with vacant niches and were readily invasible. He paid particular attention to the high levels of local variation and, believing that there was no fixed limit to *LSR* (Aho, 1990), favoured local pool saturation as the explanation for his findings. In fact, of course, both explanations may hold even within the same locality, as supply may determine the species richness of the community but interactions its composition. We thus agree with Aho (1990) in concluding that *RSR* is not normally a major determinant of *LSR* and that local communities approach saturation for other reasons. Our data, however, suggest that there are upper limits to *LSR*, even though at this stage we are unable to favour either of the possible explanations advanced for this.

The essential conclusions from the two parasite studies are therefore similar, but contrast strongly

with studies on fish assemblages. Tonn (1990) found a linear relationship between *RSR* and *LSR* for temperate fish (as did Huguény, personal communication, for African ones). Tonn adopted the view that his communities were open systems and that local patterns and processes were determined not only by local mechanisms but also by processes operating at larger spatial and temporal scales, i.e. that local communities are also controlled by larger-scale regional and historical processes. This view is increasingly being adopted by many other ecologists, e.g. Levin (1992) and Kennedy & Bush (1994). We find no evidence of this in our study on helminth communities, apart from the historical and temporal scale effects on helminths of introduced fish. We interpret the linear relationship between *RSR* and *LSR* in introduced fish as a temporary situation and reflecting the shortage of time (A.D. 1200 is taken as the earliest date of introduction: most introductions are more recent) for the community to become saturated, but it is difficult to transfer this explanation without alteration to temperate and tropical fish communities. It is more likely that the time-scales required to reach saturation in the two types of community differ and that processes operate faster on parasite communities which therefore saturate sooner. Whatever the explanation, a major consequence of this difference is in predictability of community structure. In the case of unsaturated communities, a knowledge of the *RSR-LSR* relationship provides at least a partial basis for prediction of *LSR* and changes in *RSR* will affect changes in *LSR* (Tonn, 1990): in the case of parasite communities this is clearly not the case as a knowledge of *RSR* does not improve prediction of *LSR*. *RSR* is not therefore a major or missing key determinant of helminth community structure in British freshwater fish.

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