

# The number of niches in intestinal helminth communities of *Anguilla anguilla*: are there enough spaces for parasites?

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## SUMMARY

The suggestion that there may be a limit to the number of niches available to helminth species in the intestine of *Anguilla anguilla* was investigated by examining the frequency distributions of the number of helminth species per eel and the relationships between maximum and mean infracommunity richness and component community richness in 1 locality over 17 years and in 64 localities throughout Ireland and England. The maximum number of species per eel did not exceed 4 in the 1 locality, or 3 in the 64 localities. In both the single and the several localities, the relationship between maximum and mean infracommunity richness and component community richness was curvilinear and best described by a power or polynomial function. This was interpreted to mean that infracommunity richness became increasingly independent of component community richness, and that infracommunities were saturated at values well below the higher level of helminth richness immediately available for colonization i.e. component community richness. It is argued that these findings cannot be explained by supply-side ecology, pool exhaustion or transmission rates, but only by infracommunity processes acting to impose a fixed limit to the number of species in an infracommunity. Most infracommunities are species poor, and the limiting factors will only operate as species richness rises to determine a maximum. Acceptance of a limit to the number of niches available also resolves the apparent inconsistency between the occurrence and importance of inter-specific competition and the nature of isolationist communities.

Key words: fish, helminth community, niche, competition, species richness, temporal series, spatial series.

## INTRODUCTION

Intestinal helminth communities, both infra and component, in eels *Anguilla anguilla* are species poor and characterized by low densities, low diversity, high dominance and vacant niches (Kennedy, 1985, 1990, 1993). They are thus considered to be unstructured, stochastic assemblages and isolationist in nature.

Some aspects of the community organization, however, appear not to be entirely consistent with this view. There are indications that competition may occur between some species, leading to reduction in niche overlap (Bates & Kennedy, 1990; Kennedy, 1992), though not between others (Bates & Kennedy, 1991). This would suggest that structuring processes may be playing a greater role than would generally be expected in unstructured communities. More direct evidence for the operation of structuring processes comes from 3 studies. First, Kennedy (1990) showed that infracommunities were always poorer than component communities and that the number of intestinal helminth species per eel did not exceed 3. Next, Kennedy (1993) showed that over a period of 14 years in one small river there were

major changes in component community richness and diversity, whereas the relative lack of change in species richness and diversity at infracommunity level suggested an underlying constancy of structure. Finally, Kennedy & Guégan (1994) demonstrated that local helminth communities of several fish host species including eels were saturated, and consequently local processes were important. In all 3 studies, the authors suggested a fixed number of niches in the intestine of eels as one possible explanation of their findings. A limited number of species available for infection of eels and low transmission rates were also considered, but neither structural processes in communities nor supply-side ecology could then be preferred as explanations.

This inability to prefer any one of these explanations was due in part to the limitations of the data bases, in particular the fact that too few data on infracommunities came from localities in which the component communities of eels were also rich and, in part, to the fact that none of the investigations had specifically focused on the number of niches available and occupied in eel intestines. The present investigation focuses solely on this issue. By re-visiting the data-sets of Kennedy (1990, 1993), extending the data base in coverage of space and time and adopting a novel approach to the comparison of infracommunity and component community richnesses,

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we aim to demonstrate that there are a fixed number of niches available to helminths in the intestine of eels and so there is not enough space there for parasites.

Essentially, we adopt the views and arguments of Cornell (1985*a*, 1994) and Ricklefs (1989) for the importance of local versus regional processes. Accordingly, our term component corresponds to the level of local richness as generally employed in community ecology (Strong, Lawton & Southwood, 1984; Cornell, 1985*b*; Hugueny & Paugy, 1995), and our infracommunity level to the individual richness level. We, however, address a different aspect of richness, namely how many parasite species have colonized an individual host from a local pool. Apart from the terminology, our approach is similar to those of other community ecologists, facilitating direct comparison between standardized models.

#### MATERIALS AND METHODS

The basic approach to evaluating the number of intestinal niches in eels was that suggested by Price (1984, 1990) of comparing the same host in a number of different habitats and/or in a single habitat over time. The data set of Kennedy (1990) was used as the basis for comparison of habitats, and was extended from the original 39 localities and 842 eels to 64 localities and 1276 eels captured throughout Ireland and England (Table 4). The data set of Kennedy (1993) on helminth communities in eels of the River Clyst was used as the basis for comparisons of communities over time, but now extends over 17 years and to 1175 eels (Table 2). Thus, both spatial and temporal data series are used in this analysis. Details of collection and examination methods can be obtained from Kennedy (1990, 1993).

Two methods of estimating the number of niches occupied were adopted. The first was to examine the frequency distributions of the number of parasite species per eel for grouped samples over Ireland, England and the River Clyst and, for comparative purposes only, Australian eels (data from Kennedy, 1995). The second approach was to plot maximum infracommunity richness (abbreviated hereafter to *ICR<sub>max</sub>*) and mean infracommunity richness (*ICR<sub>mean</sub>*) against component community richness (*CCR*) for all 64 localities (most spatial samples were taken in summer, but not in the same month; use of maximum parameter values will help minimize any seasonality or host size influences), and separately for the same month (April) in all years in the River Clyst. This procedure is analogous to that adopted for examining the relationship between regional species richness and local species richness (Aho, 1990; Cornell, 1994; Kennedy & Guégan, 1994) and results are interpreted in the same way. If points fall along the line of equality, infracommunity richness is directly and linearly dependent on component

community richness. If the relationship is linear, but with a slope  $< 1$ , then proportional sampling may be occurring i.e. *ICR* is always a fixed proportion of *CCR*. If, however, the points fall below the line of equality and the relationship is curvilinear and can be described by a power function, then infracommunity richness becomes increasingly independent of component community richness and infracommunities are becoming saturated at levels well below component community richness. Component community richness is then treated as an independent variable and correlated with infracommunity richness in the April samples (time series) and different localities (spatial series).

Since the shape of the relationship is of critical importance to the interpretation of the data, attempts were always made to describe the shapes of any curve as precisely as possible by fitting polynomial and power functions to the data and then testing for goodness of fit, essentially in the same manner as Kennedy & Guégan (1994). Following Cornell (1994), we took the demonstration of the existence of proportional sampling (a linear relationship, with slope  $\leq 1$ ) as a null hypothesis, since it indicates the absence of any effects of helminth species interactions on the composition and structure of the infracommunity. Time series data (R. Clyst) were not transformed before analysis, but in the case of spatial series data, all variables were  $\log_e$  transformed to meet assumptions for parametric analysis. *CCR* and *ICR<sub>max</sub>* values were  $\log_e(x+1)$  transformed (Sokal & Rohlf, 1981). In respect of the data sets from the 64 different localities, the relationships between *ICR<sub>max</sub>* and sampling effort (defined here as the number of eels per sample) and between *CCR* and number of parasite species known per region (Ireland or England) were examined initially to take account of the comments of Gregory (1990). Since relationships between both sets of variables were positive and significant, subsequent analyses used residual values to remove the effect of the specified covariates in regression procedures (Sokal & Rolf, 1981).

To test the shape of a relationship, untransformed, exponential and power function models were fitted to the data and the model that adequately linearized the relationship and accounted for the greatest proportion of the variance was accepted as the best model (Connor & McCoy, 1979). This was confirmed by visual inspection of graphical plots for the untransformed and for all transformed models. In addition, we used a scatterplot smoothing routine, a lowess function, which allows one to look for a functional relationship between *Y* and *X* without prejudging its shape (Wilkinson, Hill & Vang, 1992) and consequently illustrates the general behavioural tendency of *Y* as a function of *X*.

Analysis of data for Fig. 3 posed special difficulties in respect of how to examine the local-individual

Table 1. Frequency distributions of the number of parasite species per eel for England and Ireland combined, separate and River Clyst samples

		Number of parasite species per eel								
		0	1	2	3	4	5	6	7	
The British Isles	No. of eels	629	432	164	51	0	0	0	0	
	%	49.3	33.8	12.8	3.9	0	0	0	0	
Ireland	No. of eels	126	115	39	2	0	0	0	0	
	%	44.7	40.7	13.8	0.7	0	0	0	0	
England	No. of eels	503	317	125	49	0	0	0	0	
	%	51	32	12.5	4.5	0	0	0	0	
River Clyst (South-West)	No. of eels	732	351	72	17	3	0	0	0	
	%	62.3	29.8	6.1	1.4	0.2	0	0	0	
Australia	No. of eels	10	24	23	28	17	11	2	1	
	%	8.6	20.7	19.8	24.1	14.6	9.5	1.7	0.9	

Table 2. Variation of component and infracommunity richnesses in intestinal helminth parasite species in eels of the River Clyst (England) over time from 1979 to 1995

(*CCR* = Component Community Richness; *ICRmax* = Maximal Infracommunity Richness; *ICRmean* = Mean Infracommunity Richness across the number of eel specimens collected in the corresponding April sample, s.d., Standard deviation.)

Year	No. of samples	Total no. of eels caught	No. of eels April Sample	<i>CCR</i>	<i>ICRmax</i>	<i>ICRmean</i>	$\pm$ s.d.
1979	3	75	36	3	3	1.14	0.96
1980	5	98	27	3	3	0.67	0.72
1981	10	179	86	3	2	0.23	0.45
1982	10	201	50	3	1	0.14	0.41
1983	4	138	50	2	1	0.06	0.24
1984	2	100	50	0	0	0	0
1987	10	206	32	8	2	0.78	0.78
1991	4	101	34	9	3	1.44	0.94
1992	3	100	44	7	4	1.16	0.77
1994	1	17	17	4	2	0.82	0.80
1995	1	9	9	5	3	1.56	0.73

relationship after corrections for sample size and source pool differences. The two size, new, corrected measures of residual variables scaled logarithmically ( $X_1$ ,  $Y_1$ ) and resulting from the two size control of the original logarithmically scaled variables ( $X_0$ ,  $Y_0$ ) were then transformed into the corresponding exponential values ( $X_2$ ,  $Y_2$ ) to visualize the actual behaviour of the curves. Since both new axes were transformed independently as a function of their respective and independent covarying variables (number of species on a checklist for  $X_0$  and sampling effort for  $Y_0$ ), the new residual co-ordinates ( $X_1$ ,  $Y_1$  and  $X_2$ ,  $Y_2$ ) are scaled independently. For plotting the asymptotic model for which each  $X_2$  value is equal to the  $Y_2$  value (curve A of equality with a slope of 1: the boundary of Cornell (1994)) we proceeded in the following way. The theoretical functions which provided the best fit to all the data points were used and each of the  $X_2$ ,  $Y_2$  co-ordinates calculated. The resulting curves were drawn and the asymptotic linear line was plotted on the diagram. By

comparison of the empirical and theoretical models we were able to plot the exact position of the asymptotic linear curve (curve A) on Fig. 3.

All statistical analyses were performed using Systat version 5.2.1 (Systat, Evanston, IL) for a Macintosh.

## RESULTS

### *Frequency distributions*

Inspection of the frequency distributions of the number of helminth species per eel infracommunity reveals a very similar pattern for Ireland, England and the River Clyst (Table 1). Between 45 and 62% of eels are uninfected and the single commonest frequency amongst infected eels is 1 species per host individual. Only in the River Clyst (Tables 1 and 2) does the number of species per eel exceed 3 (in 0.2% of eels). The slight differences in frequency distribution between Ireland, England and the River

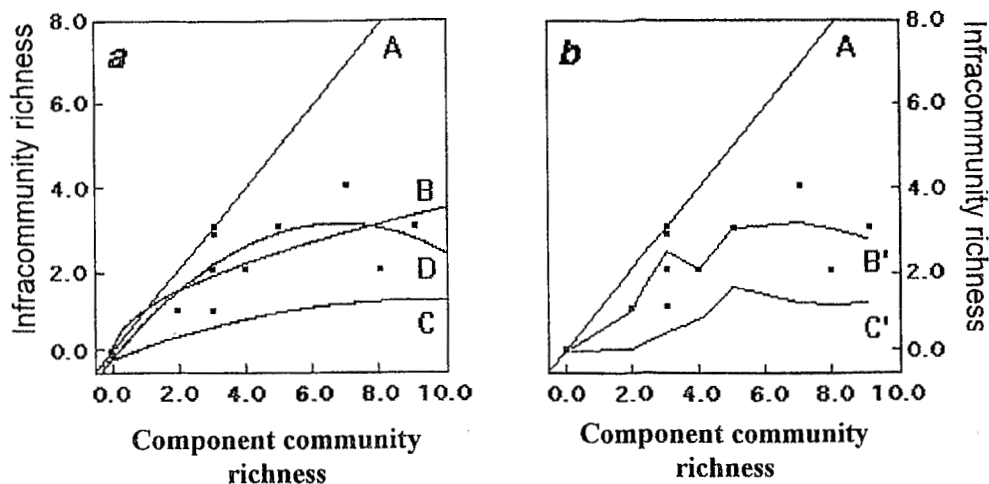


Fig. 1. Scatter diagrams of component community richness (*CCR*) versus infracommunity richness for River Clyst (South West England) data (untransformed). Fig. 1.(a) Curve A corresponds to the saturation of parasitofauna for which each plot of infracommunity richness equals that of the component community richness; curve B (double logarithmic function) and curve D (polynomial function) correspond to the behaviour of maximum infracommunity richness (*ICRmax*) values, and curve C to the behaviour of mean infracommunity richness (*ICRmean*) values. The observation of the relationships between observed values and those expected based on the above regression models shows that a combination of variables achieved a good fit to the data with no obvious signs of non-linearities for curve D ( $\chi^2 = 60$ ,  $\nu = 25$ ,  $P = 0.0010$ ). The fit was poorer for curves B ( $\chi^2 = 49.5$ ,  $\nu = 40$ ,  $P = 0.1440$ ) and C ( $\chi^2 = 96$ ,  $\nu = 88$ ,  $P = 0.2630$ ). Fig. 1.(b) Curves B' and C', corresponding to curves B and C on the left, indicate the median trends of the curves and fit a lowess function. For commodity and visibility, only plots for *ICRmax* versus *CCR* relationships are illustrated on diagrams.

Table 3. Relationships between component community richness (*CCR*) and maximum infracommunity richness (*ICRmax*), and between component community richness (*CCR*) and mean infracommunity richness (*ICRmean*) for 11 samples from the River Clyst (South West England)

(Both polynomial ( $y = 0.961x - 0.071x^2 - 0.145$ ,  $P = 0.023$ ) and double logarithmic ( $y = e^{0.173x^{0.598}}$ ,  $P = 0.002$ ) functions fit the data for the relationship *ICRmax* and *CCR*. A double logarithmic ( $y = e^{0.119x^{0.406}}$ ,  $P = 0.007$ ) function is a better fit to the data for the relationship between *ICRmean* and *CCR*. Corresponding curves are illustrated on Fig. 2.  $n$  = number of plots, D.F. = degree of freedom,  $r$  = correlation coefficient,  $r_{adj}^2$  = adjusted determination coefficient,  $x(p)$  = slope order 1 (probability-test),  $x^2(p)$  = slope order 2 (probability-test). All statistical probabilities are two-tailed.)

Maximum infracommunity richness versus component community richness									
	$n$	D.F.	$r$	$r_{adj}^2$	Intercept	$x(p)$	$x^2(p)$	F-test	$P$
Polynomial function	11	2.8	0.782	0.514	-0.145	0.961 (0.026)	-0.071 (0.078)	6.29	0.023
Logarithmic function (double transformation)	11	1.9	0.643	0.348	0.173	0.598 (0.002)	—	18.88	0.002
Mean infracommunity richness versus component community richness									
Logarithmic function (double transformation)	11	1.9	0.754	0.520	0.119	0.406 (0.007)	—	11.83	0.007

Clyst reflect differences in overall component and infracommunity richness: both tend to be poorer in Ireland than those in England, whereas the River Clyst at times contained the richest helminth communities yet known in *A. anguilla*. The value of 9 for *CCR* recorded in the R. Clyst in 1991 was not equalled in this locality at any other time (Table 2) or in any other locality (Table 4) and the highest value of *ICRmax* was also recorded in this river in 1992 (Table 2). Comparison of helminth communities of eels from Australia to these data indicates fun-

damental differences; most eels harboured at least 1 species and a maximum of 7. Data on parasite communities of Australian eels will not be considered further in this study since there are not enough data from a large enough number of localities.

#### Temporal series

The River Clyst was selected for study for two reasons: it is the only locality for which such an extensive time series of data is available (over 17

Table 4. Untransformed data for the 64 localities: the number of eel specimens analysed for parasitological investigation, their component community richness (*CCR*), their maximum infracommunity richness known per eel individual (*ICR<sub>max</sub>*), their corresponding mean  $\pm$ s.d. infracommunity richness (*ICR<sub>mean</sub>*) across the different eels collected per locality

(A line indicates no infracommunity data available.)

Region	Locality	No. of eels	<i>CCR</i>	<i>ICR<sub>max</sub></i>	<i>ICR<sub>mean</sub></i>	$\pm$ s.d.
Ireland	River Bann	9	2	1	0.33	0.50
	Lough Corrib	62	3	2	0.43	0.59
	Lough Killarney	7	1	1	0.43	0.53
	Lough Garton	6	0	0	0	0
	Lough Derg, Donegal	3	0	0	0	0
	Lough Allua	18	1	1	0.11	0.32
	Lough Bofin	8	1	1	1.00	0
	Lough Boderg	8	2	2	1.22	0.44
	Lough Coosan	8	2	2	1.40	0.55
	Lough Ree	15	3	2	1.00	0.65
	Lough Conn	20	1	1	0.05	0.22
	River Nore	28	2	2	0.65	0.74
	Lough Bunny	11	3	2	0.58	0.67
	Lough Dromore	17	3	2	1.07	0.59
	Lough Neagh	30	3	2	0.92	0.57
	Lough Derg, Clare	34	4	3	1.39	0.61
	River Shournagh	43	3	2	—	—
England	River Avon	24	3	2	0.83	0.70
	River Clyst	32	6	3	0.78	0.90
	River Culm	25	3	1	0.24	0.40
	River Douglas	35	3	2	0.68	0.60
	River Dart	30	2	1	0.13	0.30
	River Erme	30	1	1	0.17	0.40
	Exminster Marsh	18	5	3	1.90	0.60
	River Frome	10	3	1	0.60	0.50
	River Gara	20	1	1	0.05	0.20
	Jersey	19	3	3	0.84	0.90
	River Idle	16	1	1	0.75	0.40
	River Mawn	21	3	1	0.52	0.50
	River Otter	35	5	2	0.51	0.50
	River Ouse	5	1	1	0.40	0.50
	River Sheme	24	3	3	0.54	0.80
	River Stour (South)	30	4	3	0.97	0.90
	River Trent	27	1	1	0.77	0.40
	River Tyne	21	3	2	0.33	0.60
	River Wear	19	3	1	0.21	0.40
	River Wych	20	1	1	0.80	0.40
	Hanningfield Res.	21	2	2	0.52	0.70
	Shobrooke Lake	55	4	2	0.74	0.70
	Slapton Ley	35	3	2	0.70	0.70
	Driffeld Canal	25	3	2	0.32	0.50
	River Conwy	10	1	1	0.10	0.30
	River Itchen	13	3	2	0.69	0.70
	Lancaster Canal	18	3	1	0.44	0.50
	Conwy Reservoir	25	3	1	0.24	0.40
	River Ribble	18	1	1	0.05	0.20
	River Teifi	25	2	2	0.20	0.50
	Keadly Dam	48	5	3	—	—
	Black Toft Brook	16	8	3	—	—
	Kellafield	20	4	2	—	—
Reads Isl.	20	4	2	—	—	
Huntspill Dam	16	2	2	0.12	0.50	
River Avon (Hants)	18	3	2	1.00	0.35	
Bridgewater Canal	20	1	1	0.50	0.50	
Eastham Reservoir	22	3	2	0.41	0.70	
Bleadon Lake	17	2	1	0.47	0.60	
River Brue	16	2	2	0.31	0.60	
River Frome (Avon)	11	4	2	0.81	0.80	
Chard Lake	21	1	1	0.09	0.30	
River Yeo	21	2	2	0.19	0.50	
River Frome (Dorset)	21	2	1	0.55	0.50	
River Thames (London)	16	3	1	0.44	0.50	
River Thames (London)	18	6	3	0.72	1.00	
Whitewater	29	5	3	1.58	1.00	

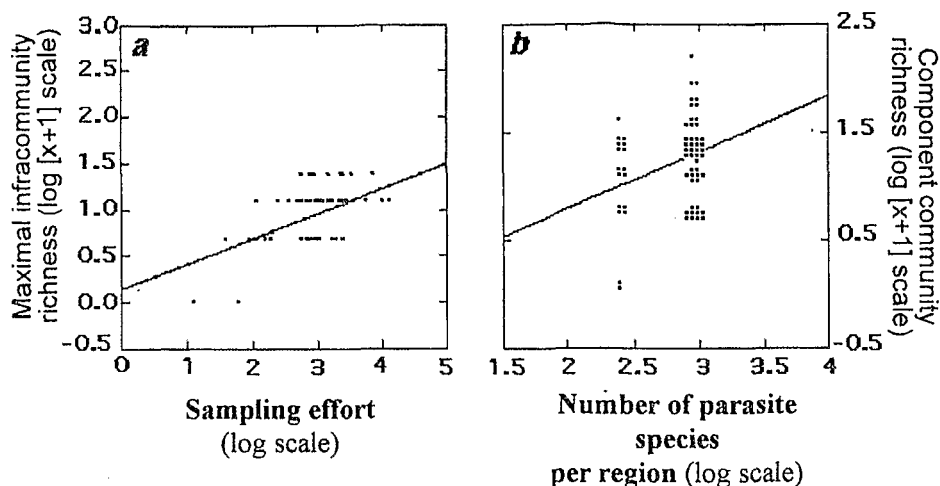


Fig. 2. (a) The relationship between maximum infracommunity richness ( $ICR_{max}$ ) values and sampling effort expressed as the number of eel specimens analysed. Maximal infracommunity richness in eel specimens increases with sampling effort across a sample of 64 British samples studied. The correlation is highly significant ( $r_{adj}^2 = 0.236$ , D.F. = 1.62, F-test = 20.438,  $P = 0.0001$ ,  $y = 0.919x + 2.066$ ). Fig. 2. (b) The relationship between component community richness ( $CCR$ ) values and number of eel parasite species based on a check-list across Ireland and England regions. Component community richness increases with the number of eel parasite species available for colonization in the region. The correlation is significant ( $r_{adj}^2 = 0.070$ , D.F. = 1.62, F-test = 5.715,  $P = 0.020$ ,  $y = 0.519x - 0.239$ ). Both axes are scaled logarithmically.

years) and over this period  $CCR$  has varied from 0 to 9 (Table 2). Despite these changes in  $CCR$ ,  $ICR_{max}$  has never exceeded 4 and even over the period from 1987 to 1995 when  $CCR$  varied between 4 and 9,  $ICR_{max}$  only varied between 2 and 4 (Table 2).

Relationships between  $ICR_{max}$  and  $ICR_{mean}$  and  $CCR$  are illustrated in Fig. 1 from which it can be seen that all the points fall on or below the lines of equality, and the relationships are not linear. No relationship between  $ICR_{max}$  and sampling effort has been observed. Fits of the relationships to a number of models are also illustrated in Fig. 1 a, b. Both polynomial and logarithmic functions (after double transformation) satisfactorily fit the data for the relationship between  $ICR_{max}$  and  $CCR$ , but the power function provides the better fit for the relationship between  $ICR_{mean}$  and  $CCR$  (Fig. 1 a, Table 3). Lowess functions for both  $ICR_{max}$  and  $ICR_{mean}$  against  $CCR$  confirm the ceiling (Fig. 1 b), to adopt the terminology of Cornell (1994), and this reinforces the view that the null hypothesis of the existence of proportional sampling or a boundary limit (curve A) can be discarded. It can therefore be concluded that the relationship between  $ICR$  and  $CCR$  is curvilinear in nature and that  $ICR$  becomes increasingly independent of  $CCR$  as the values of the latter rise whilst  $ICR_{max}$  approaches an asymptote of approximately 4.

Consideration of the composition of the richest infracommunities only i.e. those containing 3 or 4 species, indicates that there is no consistent pattern of parasite species organization. Only 15 eels fell into this group, and of these 6 harboured one species of acanthocephalan, one cestode and one nematode; 4

harboured 2 species of nematode and one of cestode and 2 harboured 2 species of nematode, one of cestode and one of acanthocephalan. Other combinations occurred only once.

#### Spatial series

Inspection of the raw data set for the 64 localities in Ireland and England (Table 4) indicates that  $ICR_{max}$  over all localities never exceeded 3 and was independent of  $CCR$  in the richest localities. However,  $ICR_{max}$  values were also positively correlated with sampling effort (Fig. 2 a) and differences in  $CCR$  values between Ireland and England reflected differences in their respective regional community richness (11 species for Ireland, 17 species for England) (Fig. 2 b).

Relationships between  $ICR_{max}$ ,  $ICR_{mean}$  and  $CCR$  following compensation for sampling effort and regional species are illustrated in Fig. 3. It is again clear that all the points fall on or below the line of equality and inspection suggests that the relationship is best fitted by a power function (Fig. 3 a). A log-log function provides the best fit for the relationship between  $ICR_{max}$  and  $CCR$ , but both logarithmic and semi-logarithmic functions provide equally good fits for the relationship between  $ICR_{mean}$  and  $CCR$ .  $ICR_{max}$  becomes increasingly independent of  $CCR$  as component communities become richer and  $ICR_{max}$  approaches an asymptote. This confirms that the relationships differ from one of proportional sampling between  $ICR$  and  $CCR$  (rejection of the null hypothesis), and they are indeed curvilinear in nature, despite the control for

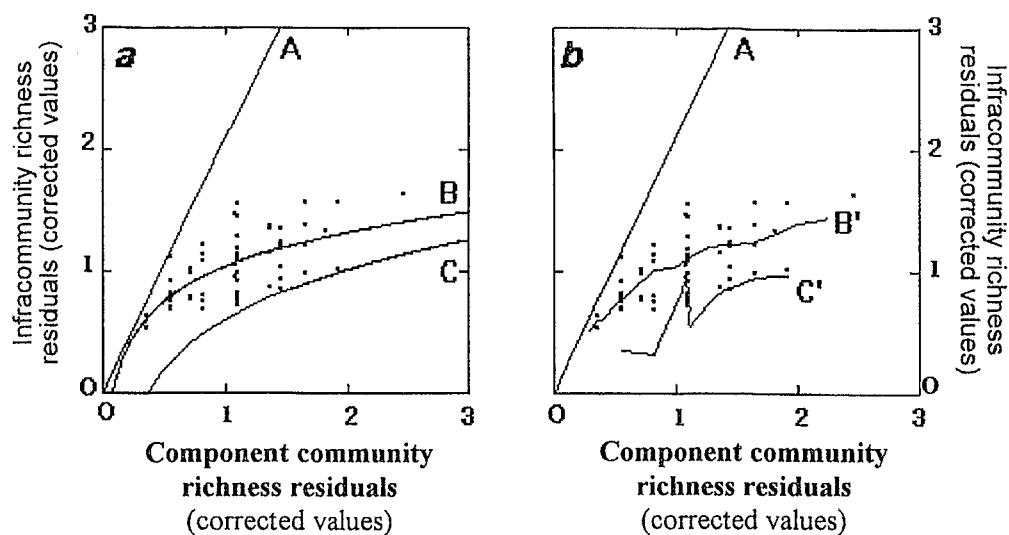


Fig. 3. Deviations from the logarithmic regression of infracommunity richnesses on sampling effort plotted against the deviations from the logarithmic regression of component community richness (*CCR*) values on eel parasite species known from a check-list per gross region. (a) Curve B ( $y = e^{0.017} \cdot x^{0.413}$ ,  $n = 64$ ,  $P = 0.0001$ ) shows maximum infracommunity richness (*ICRmax*) values, and curve C ( $y = e^{0.014} \cdot x^{0.347}$ ,  $n = 59$ ,  $P = 0.0001$ ) mean infracommunity richness (*ICRmean*) values. The observation of the relationships between observed values and those expected based on the above regression models shows that a combination of variables achieved a good fit to the data with no obvious signs of non-linearities for curve B ( $\chi^2 = 577.65$ ,  $\nu = 462$ ,  $P = 0.0001$ ), whereas the fit was poorer for curve C ( $\chi^2 = 497.97$ ,  $\nu = 528$ ,  $P = 0.8220$ ). (b) Curves B' and C', corresponding to curves B and C on the left, indicate the median trends of the curves and are derived from fitting a lowess function. For commodity and visibility, the data points illustrated on diagrams are maximum infracommunity richness (*ICRmax*) plots only. See text for details.

regional richness and sampling effort on *CCR* and *ICR* estimates respectively. The behaviour of *ICRmean* against *CCR* is similar to the above pattern, and the two curves show a general tendency toward saturation, *ICRmean* values being obviously below *ICRmax* values. Lowess function procedures yielded to the same behavioural tendencies of the curves (Fig. 3b), which tends to demonstrate again that the presence of a ceiling is characteristic of, and strongly suggestive of, an interactive infracommunity.

There appears to be no consistent pattern in the composition of the richest infracommunities. In Ireland, a pair of acanthocephalan species was the commonest combination whereas in England, a pair of acanthocephalan species and 1 nematode species was the single commonest combination.

#### DISCUSSION

As Price (1984, 1986, 1990) has discussed, determination of the number of niches available to, and occupied by, endoparasites is neither simple nor easy and estimates can only be made by comparing, as here, one host species in a number of different localities or in one locality over time. This investigation was restricted to the intestinal helminth parasites of eels, partly because of the extensive and intensive data sets available for comparisons and partly because eels were early post-glacial colonizers of the British Isles and have subsequently become widely distributed: helminth infracommunity struc-

ture does not therefore reflect time post-colonization (Guégan & Kennedy, 1993), and is relatively unaffected by biogeographical considerations. Although infracommunity data from the continent are limited, we currently find no reason to assume that parasite communities of eels differ in mainland Europe. For example, in a series of Italian lagoons Di Cave (personal communication) has found that *CCR* ranges from 3 to 6, but *ICRmax* is only 3, a finding consistent with our data. Measures of community richness should, however, be gathered to test the generality of our observations. Helminth communities in Australian eels, *A. reinhardtii*, are clearly different. They are richer and more diverse, composed primarily of digenean and nematode species and *CCR*, *ICRmean* and *ICRmax* are higher (Kennedy, 1995). Nevertheless, there are still not sufficient data from a large enough number of localities to subject them to similar analyses and to determine if there is any limit to *ICRmax* in Australian eels. At this time, the differences can only be noted and conclusions from the present study should only be applied to intestinal helminth communities of *A. anguilla* in the British Isles.

Both methods of estimating the number of niches in the eel intestine confirm the earlier indications of Kennedy (1990, 1993) that there appears to be a limit to the number of helminth species that an eel can harbour. Comparison of the frequency distribution of number of species per eel over time (R. Clyst) and space (64 localities) suggests that this limit is 4, although an *ICRmax* of 3 is very seldom exceeded.

In fact, *ICRmax* exceeded 3 in only one year in one locality, regardless of the value of *CCR*.

The most interesting feature of the relationship between *ICR* and *CCR* is that it is curvilinear, which permits the rejection of the null hypothesis of a proportional sampling between *ICR* and *CCR*. As Aho (1990) and Kennedy & Guégan (1994) argued when performing a similar analysis of the relationship between local species richness and regional species richness, if the best fit is linear and the points fall along the line of equality (curves A on diagrams), then *ICR* is directly proportional to *CCR*, *ICR* derives mainly from broad-scale processes underlying *CCR*, and the helminth communities are unsaturated. However, if the points fall below the line of equality and the relationship is curvilinear, and regardless of whether a power function or a polynomial provides the best fit, then *ICR* becomes increasingly independent of *CCR* and the infracommunities become saturated at values corresponding to the asymptote of the curve and well below those of *CCR*. Thus, *ICRmax* is not just a simple reflection of supply side ecology nor local pool exhaustion: some factor(s) is limiting *ICRmax*, and, *a fortiori*, *ICRmean*, other than broad-scale processes such as *CCR*.

When considering explanations for the similar curvilinear relationship between local and regional species richness, Kennedy & Guégan (1994) suggested two possibilities: helminth communities were structured in some way (e.g. by interspecific competition) or the situation reflected supply side ecology and local pool exhaustion, i.e. each local community richness was limited by local colonization events and was not significantly influenced by patterns on the large, regional spatial scale. Analogous explanations can be advanced for the present findings, but an explanation based on supply side ecology cannot readily be substantiated. For example, in the 1991 River Clyst sample 9 species were available to infect individual eels, yet *ICRmax* was only 3. The pool could not thus be considered to be exhausted. It is of course feasible that transmission rates may play some part in determining *ICR*. When component communities are rich, some of the species are less common and occur at low prevalence and so the probability of all 9 species occurring in a single eel must be low. This does not explain, however, why a limit of 4 species was *never* exceeded in 1175 eels from the River Clyst or in 1276 eels from the 64 localities: the limit to *ICR* still falls below what would be expected if transmission rates were the only factor responsible. Preliminary attempts were made to investigate this possibility by restricting the analysis to common helminth species only, but the relationship between *ICR* and *CCR* then became distorted and artefactual as eels from localities that were species poor and in which helminth abundances were low had to be recorded as uninfected simply

because helminth infection levels fell below the arbitrary values set for common. The most parsimonious explanation of the findings at present is that infracommunities are, in fact, structured in some way and that there is an actual limit to the number of helminth niches available in the eel intestine.

This limit would appear to be independent of time and space or indeed of the species composition of the helminth community, but to be a characteristic of *A. anguilla* in freshwaters. There was considerable variation in component community composition in time (Kennedy, 1993) and space (Kennedy, 1990) and there was just as much variation in the composition of *ICRmax*. No general pattern of helminth species composition was evident in the infracommunities, although the most frequent combination was two species of acanthocephalans and one or two members of another taxon or guild (*sensu* Bush & Holmes, 1986; Bush, 1990). There was certainly no evidence to support the rule of assemblage structure proposed by Fox (1987) that 'there is a much higher probability that each species entering a community will be drawn from a different functional group (genus, or guild) before the cycle repeats'. Any two species of acanthocephalans in an eel are certainly from the same guild, and are very likely to belong to the same genus (Kennedy & Moriarty, 1987; Kennedy, 1992).

It must be understood very clearly that in the great majority of individual eels infracommunities will be unsaturated since *ICR* will obviously fall below *ICRmax*. A limit to the number of niches only sets the maximum value of richness and it is for this reason that the analysis emphasized *ICRmax*. Acceptance of a limit to the number of niches thus does not contradict the accepted view that, in general, helminth infracommunities in eels are unstructured and isolationist in character (Kennedy, 1990) or that there are vacant niches (Kennedy *et al.* 1986): the great majority of infracommunities still harbour 2 or fewer species. Acceptance of a limit does, however, help to explain some of the findings and resolve some of the inconsistencies noted earlier. If there is a limit to the number of niches available, it is not surprising that there is evidence for resource partitioning by host and parasite site selection to avoid competition (Kennedy, 1985). It should equally be unsurprising that helminth species, particularly congeners, do compete on occasion in contemporary time for the limited niche space and attendant resources (Kennedy & Moriarty, 1987; Bates & Kennedy, 1990; Kennedy, 1992). Limitation on niche availability will provide a basic structure to infracommunities. The saturation of local component communities reported by Kennedy & Guégan (1994) may thus reflect both structural determinants at infracommunity level and pool availability i.e. both bottom up and top down processes (see also Cornell, 1994).



Infracommunity composition may well be influenced primarily by top down processes i.e. the component community pool available for colonization, but its richness will be influenced by bottom up processes (e.g. interspecific interactions and niche availability). Saturated infracommunities will thus be predictable in their richness, but not their composition.

How far these conclusions can be applied to hosts other than eels is still uncertain. However, the same inconsistencies are apparent in the helminth communities of many other species of freshwater fish. These are also considered to be isolationist in character (Kennedy, 1990), yet many are locally saturated (Guégan & Kennedy, 1993), and there is also strong evidence of resource partitioning between members of the same (Thomas, 1958) and different (Halvorsen & MacDonald, 1972) taxa in space. Competitive interactions between helminth species, frequently involving an acanthocephalan, have been reported on several occasions (Chappell, 1969; Halvorsen & MacDonald, 1972; Grey & Hayunga, 1980; Bates & Kennedy, 1990) and these have led to niche segregation and, exceptionally, exclusive distributions of species on a geographical scale (Kennedy, Bates & Brown, 1989). Even in intestinal helminth communities of marine teleosts there may be evidence of resource partitioning and interactions between species (Mackenzie & Gibson, 1970) and Holmes (1990) has drawn attention to the paradox that in the fish he studied, the helminth communities appeared to be stochastic in nature with very weak evidence only for interspecific competition, yet their predictability, persistence and stability appeared too high to be explained by stochastic processes. It would thus appear very probable that some process is providing a structure to the intestinal helminth communities of other freshwater and marine fish. The possibility that this may also be a limit to the number of niches, so causing a shortage of niche space, clearly warrants further investigation of different phylogenetic and ecological groups of hosts.

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