

Patterns of infracommunity species richness in eels, *Anguilla anguilla*

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Abstract

Between October 1999 and October 2001, a total of 510 European eels *Anguilla anguilla* were captured in 13 different samples from the rivers Thames (five locations) and Test (one location) in southern England. The relationship between parasite component community species richness (CCR) and maximum infracommunity species richness (ICR_{max}) compared with that previously observed in bird and mammal hosts. Specifically, the maximum number of parasite species occurring in infracommunities equalled or exceeded half the number of parasite species in the component community at that time, across a wide range of CCR values (2–9 parasite species). Furthermore, the frequency distribution of infracommunity richness (ICR) suggested that the species composition of infracommunities is probably random. These findings suggest that intestinal macroparasite infracommunities in eels are unsaturated and potentially species rich assemblages and, in these respects, share a fundamental similarity with the infracommunities of birds and mammals.

Introduction

Host diet appears to be a significant factor explaining parasite infracommunity species richness in fish hosts (Price & Clancy, 1983; Conneely & McCarthy, 1986). The importance of additional host factors has been stressed by Kennedy *et al.* (1986), who observed that parasite infracommunities in fish display lower species richness than in birds. Kennedy *et al.* (1986) interpreted the infracommunities of fish and birds as fundamentally different in terms of species richness, concluding that a number of host traits were essential for diverse infracommunities and that fish possessed them to a lesser degree than birds. But, the extent that these host factors overshadow similarities in parasite species richness between host groups is unclear. For instance, the parasite species available to a population of birds (and mammals), appear to be randomly distributed among those hosts (Poulin, 1996, 1998) and this situation may extend to fish

(Poulin, 1998; Kennedy, 1990; Rohde, 1991, 1994). If this hypothesis is correct, fish-parasite infracommunities would, like those in birds and mammals, be random subsets of the component community in terms of parasite species composition (and richness). This would imply that infracommunities in fish, bird and mammals share a fundamental similarity, that of random assembly. While this idea is not new, further evidence has emerged of fundamental differences in infracommunity richness (ICR) between fish and birds (Kennedy & Guégan, 1994, 1996), suggesting that while parasite species may be randomly distributed between individual fish hosts, saturating processes place an upper limit to parasite species richness in eels. Similar findings have since been observed in the infracommunities of brown trout, *Salmo trutta*, and may reflect the situation in freshwater fish in general (Kennedy & Hartvigsen, 2000).

If infracommunities are unsaturated, the highest infracommunity richness value from a sample of hosts (ICR_{max}) is predicted to be a fixed and approximately linear proportion of component community richness (CCR), i.e. proportional sampling is occurring (Cornell &

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Lawton, 1992). If infracommunities are saturated, ICR_{max} should become increasingly independent of CCR, and reach a low and distinct asymptote as CCR rises. Previous research indicates that proportional sampling best describes the ICR_{max} /CCR relationship of the bird and mammal hosts so far examined (Poulin, 1996, 1998). But Kennedy & Guégan (1996) found a curvilinear relationship between ICR_{max} and CCR; ICR_{max} reached an asymptote at 3 or 4 species, often considerably lower than CCR. Kennedy & Guégan (1996) concluded that a limited number of niches were available in the intestinal infracommunities of eels from the British Isles. These authors added that since a considerable proportion of eels were typically uninfected, and infected eels generally harboured fewer than the maximum of 3 species, vacant niches in host individuals were common and that the saturation point for these infracommunities was not often reached.

If infracommunities are random subsets of the component community, the observed frequency distribution of ICR values should follow an expected distribution generated using a random-selector null model (Janovy *et al.*, 1995). Theoretically, a non-random frequency distribution of ICR might be observed if positive or negative interactions were occurring between parasite species (Janovy *et al.*, 1995). Negative interactions might be more likely to occur if the parasite component community includes (i) many species, (ii) species at high densities, (iii) congeneric species, or (iv) species belonging to the same feeding guild (Kennedy, 1990). Positive interactions between parasite species could theoretically occur if, among other scenarios, the parasite component community includes species that share an intermediate host species (Lotz *et al.*, 1995). Since positive or negative interactions involve parasite species in combination, it is assumed that data from certain component communities (certain species combinations) will be more likely to falsify the random sub-sets hypothesis if it is incorrect, than data from others. The present study used data from two component communities that satisfied the four criteria above; each included a greater number of intestinal macroparasite species than are generally reported from eel populations, included one pair of congeners, and at least two species believed to share a single intermediate host species. Although assigning parasite species to guilds remains highly speculative, acanthocephalans and cestodes, as absorbers, are interpreted here as members of the same feeding guild.

A fundamental difference in the pattern of ICR between fish and bird/mammal host groups would be supported if eels harbour saturated parasite communities. But, if infracommunities in eels are unsaturated and form random subsets of the component community, a fundamental difference between the host groups becomes less certain. If, in addition, a similar relationship between ICR_{max} and CCR to that found in birds and mammals is observed in eels, ICR patterns between the host groups might more accurately be described as fundamentally similar. The principal study objective was to test the saturation hypothesis in eels. The same data also permitted the broader comparison of ICR patterns between eels, and birds and mammals.

Materials and methods

Sampling

Eels were captured from the river Thames using fyke nets, and from the river Test via a trap built into a weir. Eels were removed to aerated aquaria, killed with an overdose of benzocaine at maximum 4 days post-capture, and dissected as fresh specimens. All intestinal macroparasites were stored in 70% ethanol, and identified to species at a later date. At least one sample of eels was obtained from each of five lowland locations on the river Thames: Windsor and Richmond (freshwater), Greenwich (estuarine), Erith and Thurrock (estuarine). Eels from the river Test were captured at Leckford. The sampling period extended from October 1999 to October 2001.

Testing the saturation hypothesis

In keeping with the methods employed by Kennedy & Guégan (1994, 1996), this particular analysis was in two stages. Initially eel samples were pooled, and the frequency distributions of ICR for (i) all eels, (ii) Thames eels, and (iii) Test eels were compared visually with the proposed upper limit. This initial examination was for qualitative comparison between sample groups and with the literature. The second stage of the saturation analysis used data from 13 eel samples to examine the form of the relationship between ICR_{max} and CCR. Additional ICR_{mean} /CCR analyses were not conducted since ICR_{mean} is particularly sensitive to seasonal fluctuation. As with Kennedy & Guégan's (1996) analysis, this study used a null hypothesis of proportional sampling (Cornell & Lawton, 1992), that is, a linear relationship between the variables with slope < 1 (ICR_{max} is always a fixed proportion of CCR). ICR_{max} and CCR data did not require transformation before analyses, which regressed linear, logarithmic and power functions for the line or curve that explained most of the variation in the data and returned the highest significance level.

Testing the random subsets hypothesis

The null model devised by Janovy *et al.* (1995) was used to test for randomness in the observed ICR frequency distribution from each sample of eels. This model considers parasite species prevalence as an indicator of the likelihood of encounter with hosts, and calculates expected frequencies using observed prevalence data. In doing so, the expected frequency distribution reflects the differing likelihood of infection with each parasite species, not simply the number of parasite species in the component community. The model does not identify parasite species or the individual infracommunities affected, considering only trends in ICR within a sample of hosts. If repeatable, significant deviation from the expected frequency distribution may suggest certain factors are operating to non-randomly shape ICR, although revealing the causes would require different analyses (Janovy *et al.*, 1995). Expected ICR frequency distributions were generated for 11 eel host samples that were suitable in terms of number of hosts and ICR data;

Erith and Richmond samples did not contain sufficient hosts for use with Janovy's model and were omitted from this analysis. Non-parametric tests were conducted on untransformed ICR data.

Results

Eel samples

In total, 510 eels were captured from six sites (table 1). Each sample of hosts contained 11–51 eels, and 11 samples contained >30 eels.

The saturation hypothesis – part 1

The first stage of the saturation analysis examined the frequency distributions of ICR for all eels, and per grouped sample, i.e. Thames freshwater eels, Thames estuarine eels, and Test freshwater eels (fig. 1). While each group had a different modal ICR class, there was no suggestion that infracommunities might be saturated, with ICR_{max} reaching 5 at the Test, and 6 in both Thames groups. When the study eels were pooled, ICR became more evenly distributed (fig. 1), but bore no obvious similarity to either the British Isles or the Clyst distributions (fig. 2) of Kennedy & Guégan (1996). When the study samples were pooled according to river only, the differences became more marked (fig. 2). Both the Test and Thames eel samples included a greater percentage of multiple parasite species infections than either the British Isles or the Clyst studies, but differed from one another in the percentage of zero and single species infections observed (fig. 2). Overall, Thames eels harboured richer

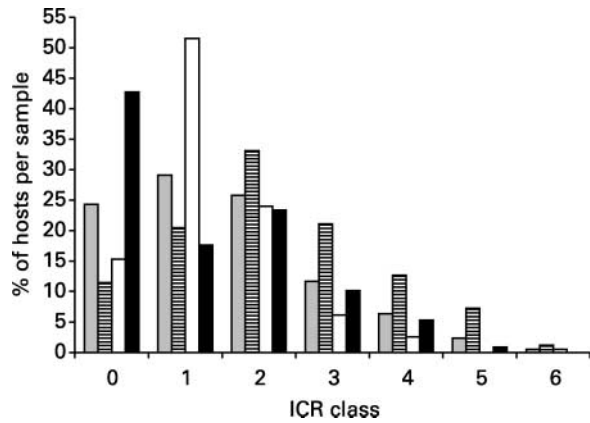


Fig. 1. The percentage frequency distribution of infracommunity species richness (ICR) for Thames and Test eels captured during 1999–2001. ■, All eels (n = 510); ▨, Thames, freshwater (n = 178); □, Thames, estuarine (n = 105); ■, Test (n = 227).

infracommunities than Test eels, and Test eels were richer than those from the published studies.

The saturation hypothesis – part 2

The ICR_{max} values found in excess of 4 species challenge the saturation hypothesis but say nothing about the form of the relationship between ICR_{max} and CCR. Testing the saturation hypothesis required fitting the line or curve of best fit between the two variables for contrast with the null model of proportional sampling (straight line with slope < 1). Three fits returned statistically

Table 1. Intestinal macroparasite species recovered from Thames and Test eels during 1999–2001.

	River Thames								River Test				
	Windsor				Ri	Gr	Er	Th	Leckford				
	Aug 2000	Apr 2001	Jul 2001	Oct 2001	Jul 2000	Jun 2001	Jun 2001	Oct 2001	Oct 1999	Jun/Jul 2000	Sep 2000	Aug 2001	Oct 2001
<i>Acanthocephalus anguillae</i>	•	•	•	•				•					
<i>Acanthocephalus lucii</i>	•	•	•	•	•			•	•			•	•
<i>Pomphorhynchus laevis</i> (estuarine)						•		•					
<i>Pomphorhynchus laevis</i> (freshwater)	•	•	•	•	•	•	•	•					
<i>Echinorhynchus truttae</i>									•	•	•	•	•
<i>Neoechinorhynchus rutili</i>										•	•	•	•
<i>Bothriocephalus claviceps</i>	•	•	•	•				•	•	•	•	•	•
<i>Proteocephalus macrocephalus</i>	•	•	•	•				•	•				
<i>Raphidascaris acus</i>		•						•	•	•		•	
<i>Goezia inermis</i>			•					•	•				
<i>Camallanus lacustris</i>		•	•										•
<i>Paraquimperia tenerima</i>	•	•		•							•	•	•
<i>Cucullanus truttae</i>										•			
<i>Spinitectus inermis</i>									•				
<i>Deroprista inflata</i>								•					
<i>Nicolla gallica</i>	•	•	•	•								•	
CCR	7	9	8	7	2	8	5	6	4	8	4	7	5
ICR _{max}	5	6	5	4	2	6	2	3	3	5	4	4	3
n eels	50	51	32	33	12	44	11	50	50	50	49	50	30

Ri, Richmond; Gr, Greenwich; Er, Erith; Th, Thurrock.

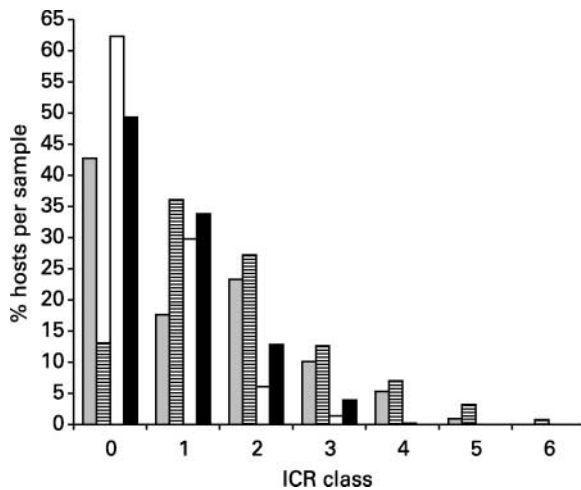


Fig. 2. The percentage frequency distribution of infracommunity species richness (ICR) from the study eels, and comparison with those from the river Clyst and the British Isles (*as reported by Kennedy & Guégan, 1996). ▨, River Test; □, River Thames; □, River Clyst*; ■, British Isles*.

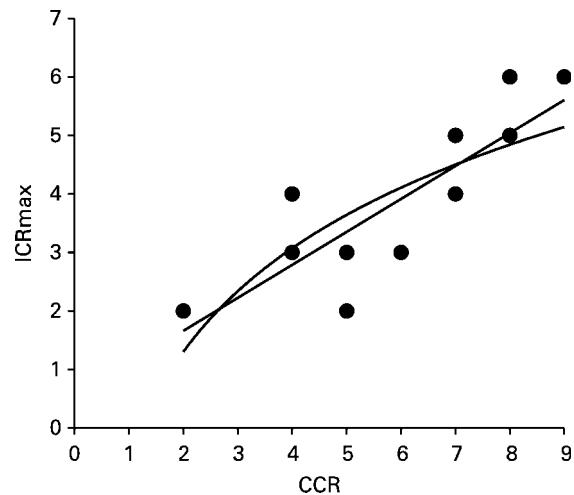


Fig. 3. The relationship between maximum infracommunity species richness (ICR_{max}) and parasite component community richness (CCR) as described by linear ($R^2 = 0.74$) and logarithmic ($R^2 = 0.65$) functions. Constructed from 13 data-points (two are duplicated, see table 1).

significant results: linear, logarithmic and power functions (table 2). Of these, the linear function had a slope estimated at 0.54, explained more variation in the data (highest R^2), and returned the (joint) highest significance level. The intercept was also realistically close to the origin with the linear function. Logarithmic and power functions also described the relationship between ICR_{max} and CCR with significant results, but did not support the saturation hypothesis since neither could be described in terms of a pronounced curve or asymptote. Figure 3 displays the linear and logarithmic functions on untransformed data (the power function is omitted for clarity).

The random subsets hypothesis

In 7 of 11 eel host samples, the observed ICR frequency distribution followed the expected distribution generated by the random-selector model of Janovy *et al.* (1995). In the remaining four eel host samples the frequency distribution of ICR deviated significantly from the random expected distribution (table 3). However, the test statistic for one of these non-random ICR frequency distributions (Leckford, August 2001 host sample) was borderline and rejected; the ICR frequency histogram also appeared to be a reasonable fit to the random model in this case (fig. 4b). The remaining non-random ICR

distributions were from eels from the Thames (Windsor, August 2000, and Greenwich, June 2001) and the Test (Leckford, September 2000).

The non-random ICR frequency distributions observed in the Windsor and Greenwich eels both contrasted with their expected distribution in a broadly similar fashion. In each case (fig. 5) the observed modal class was lower than expected, and the number of eels in the highest expected ICR class (5 parasite species) was exceeded. At Greenwich the highest expected ICR class (4 parasite species) was exceeded: a single eel harboured 6 parasite species. A similar situation was observed among Leckford eels during September 2000: the highest expected ICR class (2 parasite species) was exceeded. In this case some eels harboured 3 and 4 parasite species. The ICR frequency distribution from these Leckford eels also had a pronounced right skew which, it was felt, reflected the lower prevalence of parasite species observed during September (the Windsor and Greenwich eels were sampled in August and July respectively).

Discussion

This study observed that ICR_{max} in eel hosts was best described as a fixed proportion of CCR, and the

Table 2. Significant relationships between the maximum parasite infracommunity species richness (ICR_{max}) and parasite component community richness (CCR) from Thames and Test eels 2000/1 (using the 13 data points shown in table 1).

	R^2	Constant	Slope	F_{test}	P_{fit}
Linear function	0.74	0.699	0.54(x)	37.309	0.002
Logarithmic function	0.65	-0.335	2.486Ln(x)	24.723	0.003
Power function	0.66	1.11	0.698(x) ^{0.7117}	26.116	0.002

Table 3. Frequency distribution of infracommunity species richness (ICR) within eel host samples that were sufficiently large for analysis using the model of Janovy *et al.* (1995).

Eel sample site	Date	CCR	$\sum\chi^2$ (d.f.)	P_{fit}	Observed ICR frequency distribution
Windsor	Aug 00	7	28.35 ₍₄₎	<0.01	Non-random
Windsor	Apr 01	9	5.84 ₍₆₎	>0.05	Random
Windsor	Jul 01	8	8.70 ₍₅₎	>0.05	Random
Windsor	Oct 01	7	3.65 ₍₄₎	>0.05	Random
Thurrock	Oct 01	6	2.01 ₍₃₎	>0.05	Random
Greenwich	Jun 01	8	18.61 ₍₆₎	<0.01	Non-random
Leckford	Oct 99	4	2.58 ₍₃₎	>0.05	Random
Leckford	Jul 00	8	9.52 ₍₅₎	>0.05	Random
Leckford	Sep 00	4	12.58 ₍₄₎	<0.05	Non-random
Leckford	Aug 01	7	11.55 ₍₄₎	<0.05	Non-random
Leckford	Oct 01	5	1.92 ₍₄₎	>0.05	Random

null hypothesis of proportional sampling (unsaturated communities) was accepted. No evidence for saturated parasite communities emerged in the eels used in this study and the phenomenon, if it exists, is not nationwide. Findings from the saturation analysis were also suitable for comparing ICR patterns in eels with those from birds and mammals described in previous studies, in a manner that controlled for the richer component communities generally reported with bird and mammal host populations (Poulin, 1998). As mentioned, ICR_{max} in eels followed the same pattern

found in the bird and mammal hosts so far examined, demonstrating a linear relationship with CCR. But in addition, the slope of this linear relationship in eels was estimated at 0.54, and compares with the slope value of 0.5 previously reported from bird and mammal hosts (Poulin, 1998).

The second part of this study sought evidence that parasite species were distributed randomly, by investigating the ICR frequency distribution from a sample of eels. A random ICR frequency distribution was observed

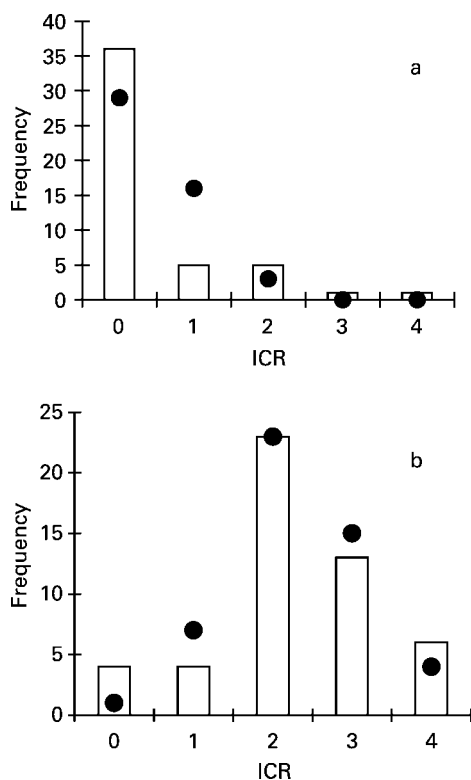


Fig. 4. Non-random infracommunity species richness (ICR) distributions observed Test (Leckford) eels during (a) September 2000, and (b) August 2001. □, Observed; ●, expected.

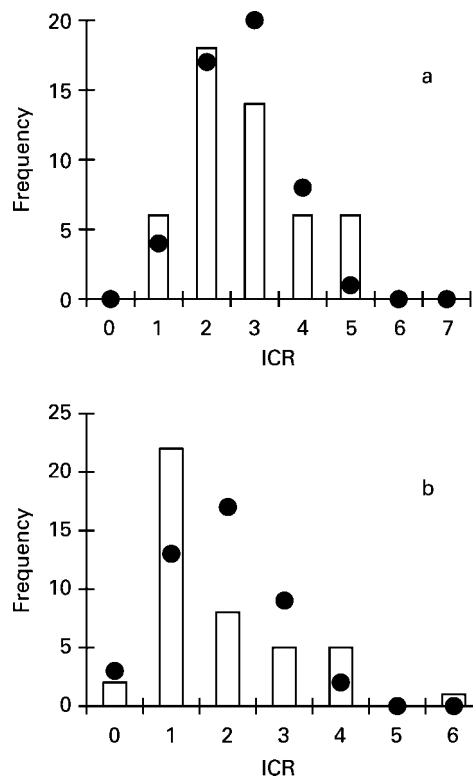


Fig. 5. Non-random infracommunity species richness (ICR) distributions observed in Thames eels from (a) Windsor, during August 2000 and (b) Greenwich during June 2001. □, Observed; ●, expected.

within 7 of 11 eel samples investigated. Of the four significantly non-random ICR distributions, one from Leckford eels (August 2001) was borderline significant. In addition, the observed ICR distribution in this case offered an acceptable (visual) fit with the expected ICR distribution; the significant result was clearly not reliable. Of the remaining three non-random ICR frequency distributions, those from Leckford (September 2000) and Windsor (August 2000) were not replicated in comparable samples from those sites, and additional samples from Greenwich have yet to be gathered. No clear common trend was observed among the non-random samples, and no biological interpretation could be confidently attached to these findings. In summary, the evidence for non-randomness found in 4 of 11 samples was not consistent or replicated, and the null hypothesis that species are randomly distributed among eel infracommunities was accepted. Caution is required however, since limitations of the null model suggest the probability of a type 2 error will be high. In addition, the random subsets hypothesis will not always apply (Poulin, 2001) and, until parasite species combinations are tested for nested subsets (rather than species richness values), a non-random distribution of parasite species among a population of hosts remains possible (Poulin & Guégan, 2000).

In conclusion, findings suggest that: (i) the intestinal infracommunities of eels are unsaturated and potentially rich parasite assemblages, where ICR is limited only to the number of parasite species available; and (ii) the parasite species combinations within infracommunities probably form random subsets of those in the component community. In these respects, the infracommunities of eels compare with those recorded from birds and mammals, and suggest a fundamental similarity in the processes by which richness is acquired by these hosts.

Acknowledgements

Dr Neil Morley of Royal Holloway, Guy Robinson of the Leckford estate, The Linnean Society and The John Spedan Lewis Trust for the Advancement of Science are thanked for support during the project.

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(Accepted 9 October 2003)

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