Comparison of richness and diversity of macroparasite communities among eels from Nova Scotia, the United Kingdom and Australia

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SUMMARY

Species richness and diversity of macroparasite assemblages were compared among American eels (*Anguilla rostrata*) from Nova Scotia, European eels (*A. anguilla*) from the United Kingdom (Kennedy, Bush & Aho, 1986; Esch *et al.* 1988; Kennedy, 1990, 1993), and Australian eels (*A. reinhardtii*) from Queensland (Kennedy, 1995). Community richness and diversity of the macroparasite fauna of American and European eels did not differ significantly for total parasite component communities, intestinal parasite component communities, and intestinal parasite infracommunities. The similarities in richness and diversity between the parasite communities of American and European eels are not surprising given the common, recent origin of these sister species. However, differences in species composition were noted between Nova Scotia and the UK. Both species of eels were infected by a nearly identical suite of specialists, but differences occurred in the species number and composition of generalist parasites. In addition, generalist species were rarely dominant in Nova Scotia, but commonly so in the UK. These differences can be attributed to the differences in the freshwater fish fauna and their parasites that occur between Nova Scotia and the UK. American and European eels are derived from a common ancestor and, whereas they have carried with them a common suite of specialist parasites during their brief period of independence, they acquired different suites of generalists apparently from their respective continental faunas after they diverged. In contrast, parasite communities of American and European eels were significantly less diverse and speciose than those of Australian eels regardless of scale (total component community, intestinal component community, intestinal infracommunity). These results support the notion that parasite communities have had more time to evolve and/or that tropical conditions have promoted parasite speciation in Australian eels.

Key words: *Anguilla rostrata*, helminth communities, diversity, species richness, Nova Scotia.

INTRODUCTION

Few data exist in the ecological literature comparing communities across biogeographical regional scales (Schluter & Ricklefs, 1993). Within the context of parasite communities, we know of only 1 study using original data. Kennedy (1995) demonstrated that individual eels (*Anguilla reinhardtii*) in Queensland, Australia, have parasite infracommunities and component communities more speciose than those in eels (*A. anguilla*) from the United Kingdom. He suggested 2 alternative hypotheses, the time hypothesis and the latitude hypothesis, as a causal explanation for the differences.

Among parasites, latitudinal gradients have been observed within species and genera of Monogenea, genera of Digenea (Rohde, 1984), as well as all metazoan ectoparasites (Rohde, Hayward & Heap, 1995) parasitizing marine fishes. There are numerous hypotheses to explain why species richness is high in the tropics (Rohde, 1992). Many are unsatisfactory or circular (Pielou, 1979; Rohde, 1992), but increased evolutionary rates (Rohde, 1992) or increased host feeding rates (Kennedy, 1995) in the lower latitudes could account for the patterns observed, at least among parasite communities. In the case of eels, enhanced species richness and diversity in Australia may also be attributed to the time a host species has spent in a biogeographical region (Kennedy, 1995).

We expand Kennedy's (1995) comparison of parasite faunas of eels across continents by analysing parasite community structure in American eels (*A. rostrata*) from Nova Scotia and comparing it to that in eels from Australia (Kennedy, 1995) and, in particular, that from the British Isles (Kennedy, Bush & Aho, 1986; Esch *et al.* 1988; Kennedy, 1990, 1993). Both Nova Scotia and the British Isles are boreal in nature, whereas Queensland, Australia is tropical. Nova Scotia is located at slightly lower latitudes (44–46° N vs. 50–56°) than the UK, but experiences cooler temperatures presently (Critch-

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field, 1966) and historically during the last ice age (CLIMAP Project Members, 1976). Nova Scotia was covered by ice during the most recent glaciation 13000 years ago (Pielou, 1991), and the British Isles experienced oscillations from glacial to interstadial to glacial conditions between 14000 and 10000 years ago (Atkinson, Briffa & Coope, 1987). The parasite communities in European and American eels can be assumed to be of similar historical age, as eels in both Nova Scotia and the British Isles are post-glacial colonizers, both areas being glaciated at relatively the same time.

European and North American eels are sister species (Avise *et al*. 1986, 1990) derived from a common ancestor. They share 6 host-specific species of freshwater parasite. Given the relatively similar climates and geological history, parasite communities in American eels should be similar to European eels. Thus, inferences will be drawn regarding the evolution of eel communities in North America and Europe after divergence from a common ancestral community since the last glaciation (Marcogliese & Cone, 1993). Furthermore, analysis of parasite community structure of American eels in Nova Scotia and comparison with communities of eels in Europe and then Australia will permit us to examine whether the time and latitude hypotheses proposed by Kennedy (1995) are applicable across an additional continent.

MATERIALS AND METHODS

We collected eels by electrofishing from 24 separate sites in Nova Scotia in 1989–93. At some sites eels were collected in more than 1 year, giving a total of 36 sites. Eels were necropsied and all macroparasites (platyhelminthes, nematodes, acanthocephalans and copepods) were removed and identified. Data on the distribution and abundance of each species, along with a description of sampling techniques, sites and necropsy protocols, have been presented by Marcogliese & Cone (1996).

Analysis of community structure at the component and infracommunity levels was carried out as described by Kennedy (1995) for total macroparasite communities and intestinal helminth communities. For each total component community, we measured the total number of parasite species, the number of allogenic species, the proportion of autogenic individuals, the mean number of species/eel, the mean number of parasites/eel, and the Berger–Parker Dominance Index. For each intestinal component community, we measured the percentage of eels infected, the total number of helminth species, the Berger–Parker Index of Dominance, and the Simpson's ($1/D$) and Shannon–Wiener Diversity Indices. For component communities, indices were generated by summing all hosts together from a site and calculating a composite value, with the exception of the mean number of species/eel, which was calculated using each host infracommunity as a separate observation. For intestinal infracommunities at each site, we measured the mean and maximum species richness/eel, the mean and maximum number of worms/eel, the mean and maximum Brillouin's Index, and the proportion of eels with 0–1 species. Determination of all indices is according to Magurran (1988), using natural logarithms when appropriate. These values were then compared to corresponding values for the UK derived from Kennedy *et al*. (1986), Esch *et al*. (1988), and Kennedy (1990, 1993), and for Australia from Kennedy (1995).

Mean measurements were compared among the 3 biogeographical regions (Nova Scotia, United Kingdom, Australia) using a non-parametric comparison of means, the Kruskal–Wallis test (SAS PROC NPAR1WAY), followed by a comparison between specific groups using the Dunn Procedure (Rosner, 1990). Only those measurements for which $\geqslant 10$ data points were available in each biogeographical region were used to determine means examined in the statistical analysis. Because of the possibility of pseudoreplication derived from using replicate measurements from the same sites in Nova Scotia and the potential bias introduced by effects of pH (see Marcogliese & Cone, 1996), for analysis and graphics we used only 1 measurement from each site. We used measurements from 1990 when available, because more sites were sampled in 1990 than any other year. If no data were available for 1990, we used the first year sampled from replicated sites. Data used in the analysis include three streams of pH $< 4{\cdot}7$, eight streams of pH 4·7–5·0, six streams of pH 5·1–5·4, and six streams of pH $> 5{\cdot}4$. Kennedy (1993) provided data for 9 years from the River Clyst. We incorporated all these data into our analyses because there are no discernible biases in the UK from any sort of gradient such as pH as in Nova Scotia. While we acknowledge the potential of pseudoreplication, the River Clyst changed substantially from year to year over the course of the study and was subjected to increasing anthropogenic influence (Kennedy, 1993), and we consider the data points independent. Selection of only 1 year would reduce the data set to a size where no reasonable statistical comparisons of total component communities or intestinal infracommunities using eels from the United Kingdom would be possible. We used a Bonferroni-adjusted P value to minimize the chance of committing a Type I error, that is, of rejecting a true null hypothesis of no difference among regions.

The term prevalence refers to the proportion of eels infected with any parasite, expressed as a percentage. Specialists are defined as those parasites which occur and reproduce almost exclusively in eels

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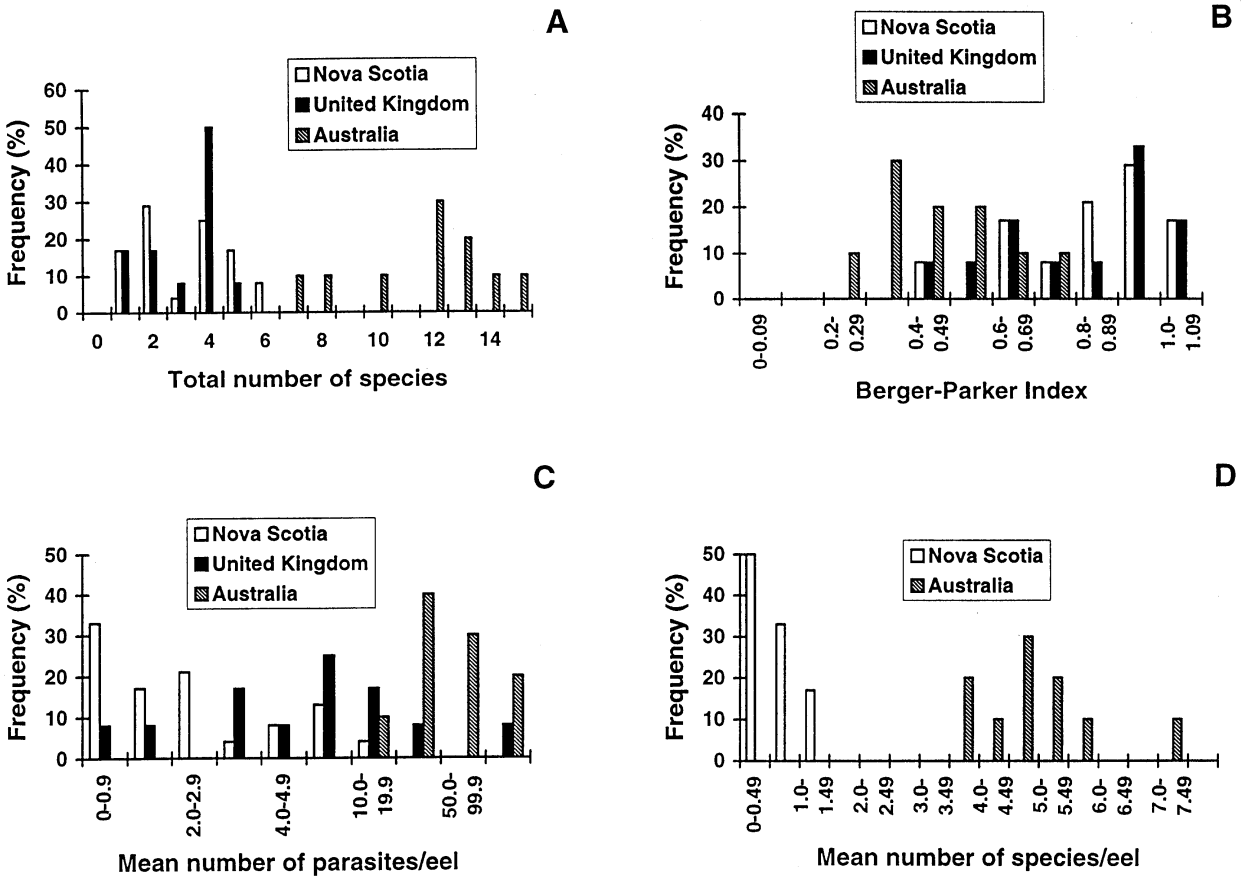

Fig. 1. Frequency distributions of various measurements of parasite species richness and diversity from total component communities of American eels (*Anguilla rostrata*) from Nova Scotia, European eels (*Anguilla anguilla*) from the United Kingdom (Esch *et al.* 1988), and Australian eels (*Anguilla reinhardtii*) from Australia (Kennedy, 1995). (A) Frequency distribution, expressed as a percentage, of species richness as measured by the total number of macroparasite species. (B) Frequency distribution, expressed as a percentage, of macroparasite diversity (or dominance) as measured by the Berger–Parker Index. (C) Frequency distribution, expressed as a percentage, of macroparasite diversity as measured by the mean number of parasites/host. (D) Frequency distribution, expressed as a percentage, of macroparasite diversity as measured by the mean number of species/host.

(see Marcogliese & Cone, 1993), whereas generalists are those which commonly occur in other families of fish (as per Margolis & Arthur, 1979).

RESULTS

Total component communities

For all measurements, means were highest (or lowest) in Australia and lowest (or highest) in Nova Scotia. The total number of species occurring in Nova Scotian eel component communities overlapped greatly with those from the UK, but only slightly with those from Australia (Fig. 1A). The Berger–Parker Indices overlapped among the 3 regions, but the range of values extended much lower (i.e. less dominance) in eels from Australia (Fig. 1B). The mean number of parasites/eel was generally lower in Nova Scotia and the UK than in Australia (Fig. 1C). For all 3 measurements, there were significant differences among regions ($P < 0{\cdot}0001$), with Australia ($n = 10$) being higher (or lower) than Nova Scotia ($n = 24$) and the British Isles ($n = 12$). The mean number of species/eel in Nova Scotia was much lower than in Australia, without overlap (Fig. 1D). Data were not available for the UK.

The dominant species among component communities in Nova Scotia was always autogenic. Usually it was *Paraquimperia tenerrima* ($n = 27$) or *Ergasilus celestis* ($n = 4$), but could be *Pomphorhynchus bulbocolli* ($n = 1$), *Echinorhynchus lateralis* ($n = 1$), *Azygia longa* ($n = 1$) or *Crepidostomum brevivitellum* ($n = 2$) (see Appendix 1). In the UK usually it was an acanthocephalan or *Pseudodactylogyrus* sp. (Esch *et al.* 1988), and in Australia *Eustrongylides* sp. or *Pseudodactylogyrus bini*, but many others could be dominant (Kennedy, 1995). In total component communities of eels in Nova Scotia, the number of allogenic species was usually 0 (83% of sites), and never greater than 1 (see Appendix 1). In the UK, it was usually 0 or 1 (Esch *et al.* 1988), whereas in Australia it was 0–2, but usually 1 (Kennedy, 1995). The proportion of autogenic individuals in eels from Nova Scotia was usually

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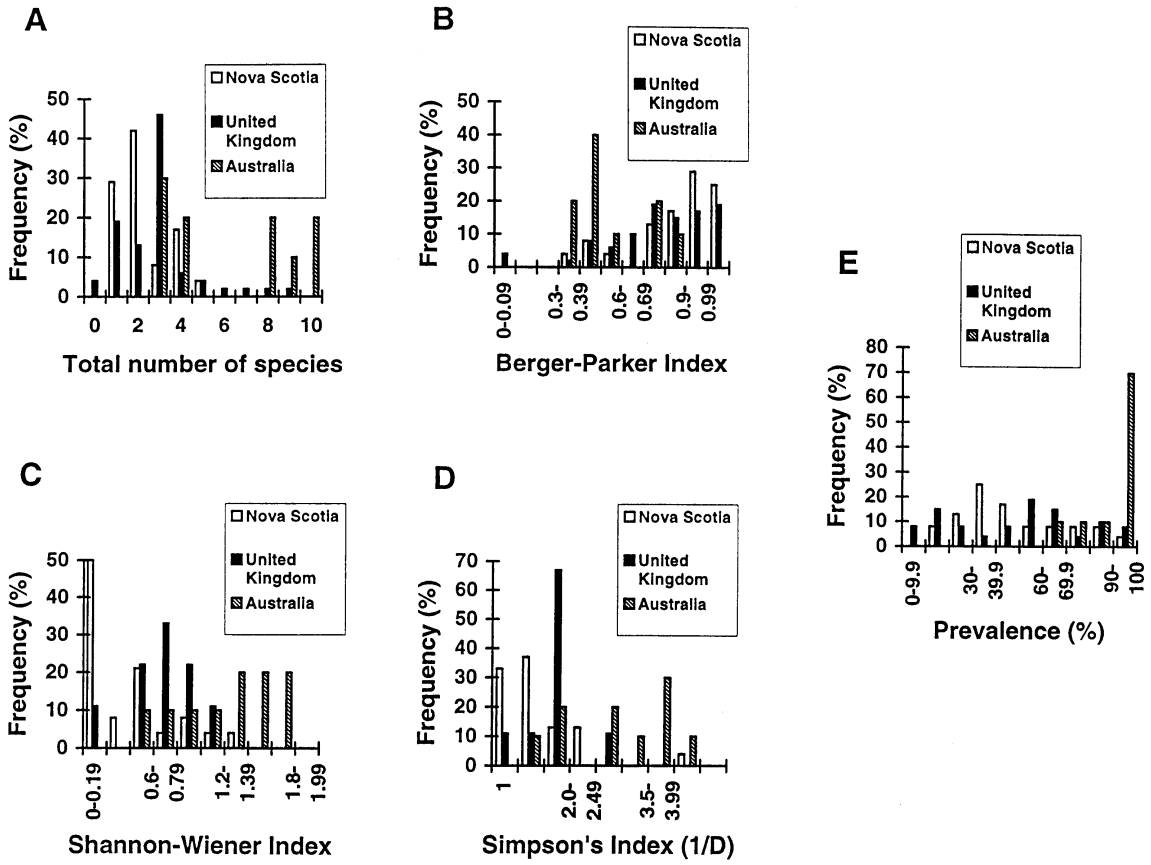

Fig. 2. Frequency distributions of various measurements of parasite species richness and diversity from intestinal component communities of American eels (*Anguilla rostrata*) from Nova Scotia, European eels (*Anguilla anguilla*) from the United Kingdom (Kennedy, 1990, 1993), and Australian eels (*Anguilla reinhardtii*) from Australia (Kennedy, 1995). (A) Frequency distribution, expressed as a percentage, of species richness as measured by the total number of macroparasite species. (B) Frequency distribution, expressed as a percentage, of macroparasite species diversity (or dominance) as measured by the Berger–Parker Index. (C) Frequency distribution, expressed as a percentage, of macroparasite species diversity, as measured by the Shannon–Wiener Index. (D) Frequency distribution, expressed as a percentage, of macroparasite species diversity, as measured by the reciprocal of the Simpson's Index. (E) Frequency distribution, expressed as a percentage, of prevalence of macroparasite infections.

100 % (83 % of sites), and never less than 95 % (see Appendix 1). In the UK, it was usually greater than 90 %, but could be much lower (Esch *et al*. 1988), and in Australia it ranged from 30 to 100 %, being less than 90 % in half the communities (Kennedy, 1995). Infection parameters for parasite component community of eels at individual sites in Nova Scotia are presented in Appendix 1.

Intestinal component communities

For all measurements, means were highest (or lowest) in Australia and lowest (or highest) in Nova Scotia. The total number of species in eel communities (Fig. 2A), dominance as measured by the Berger–Parker Index (Fig. 2B) and prevalence of parasitic infection in eels (Fig. 2E) overlapped among the 3 regions. For the 3 measurements, there were significant differences among regions ($P <$ 0·0001), with Australia ($n = 10$) being higher (or lower) than Nova Scotia ($n = 24$) and the British Isles ($n = 48$). Diversity of the intestinal component communities as measured by Simpson's and Shannon–Wiener Indices tended to be greatest in eels from Australia and lowest in those from Nova Scotia (Fig. 2C and D), but not enough data points were available for a statistical comparison.

The dominant type of parasite was usually a nematode (86 %) in eels from Nova Scotia, but could be an acanthocephalan ($n = 1$), trematode ($n = 2$) or cestode ($n = 1$) (see Appendix 2). In the UK it was usually an acanthocephalan, but nematodes also dominate frequently (Kennedy, 1990, 1993). In Australia, the dominant helminth in intestinal component communities was always a trematode or nematode (Kennedy, 1995). Infection parameters for intestinal component communities of eels at individual sites in Nova Scotia are presented in Appendix 2.

Intestinal infracommunities

For all measurements, means were highest (or lowest) in Australia and lowest (or highest) in Nova

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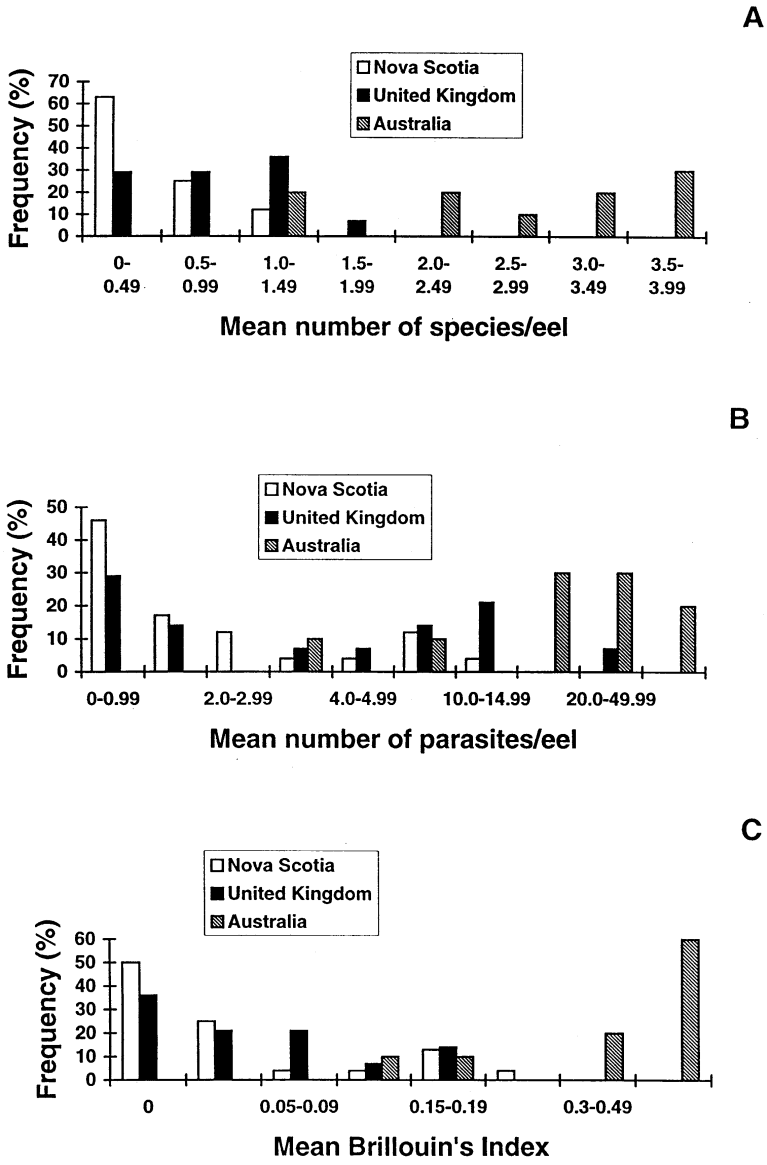

Fig. 3. Frequency distributions of various measurements of parasite species richness and diversity from intestinal infracommunities of American eels (*Anguilla rostrata*) from Nova Scotia, European eels (*Anguilla anguilla*) from the United Kingdom (Kennedy *et al*. 1986; Kennedy, 1993), and Australian eels (*Anguilla reinhardtii*) from Australia (Kennedy, 1995). (A) Frequency distribution, expressed as percentage, of macroparasite species diversity as measured by the mean number of species/host. (B) Frequency distribution, expressed as a percentage, of macroparasite abundance as measured by mean number of macroparasites/host. (C) Frequency distribution, expressed as a percentage, of macroparasite species diversity as measured by the Brillouin's Index.

Scotia. The mean number of species/eel in Australian infracommunities was consistently greater than those from Nova Scotia or the UK (Fig. 3A). The maximum number of species/eel usually ranged from 3 to 7 in Australia (Kennedy, 1995), in the UK from 1 to 3 but reached 4 (Kennedy, 1993), and in Nova Scotia 1–2 ($n = 31$), but reached 3–4 on occasion (see Appendix 3). The mean number of parasites/eel overlapped among the 3 regions (Fig. 3B). The maximum number of worms/eel intestinal infracommunity in Nova Scotia was less than or equal to 10 in 50% of the sites, and greater than 20 in only 22% of the sites (see Appendix 3). The maximum in the UK sites was usually 25–50 worms (Kennedy, 1995; Kennedy *et al*. 1986), and in Australia more than 50 in 70% of the sites (Kennedy, 1995). The mean Brillouin's Index usually was higher in intestinal infracommunities of eels from Australia than in those from the other 2 regions, where there was much overlap (Fig. 3C). In Nova Scotia, the maximum Brillouin's Index exceeded 0·1 in only 22% of the sites, and only 1 site possessed a value greater than 0·2 (see Appendix 3). In the UK, the maximum Brillouin's Index often exceeded 0·3, and reached 0·98 (Kennedy, 1993, 1995; Kennedy *et al*. 1986). Among Australian sites, the maximum Brillouin's Index of eel intestinal infracommunities always was greater than 0·5, and in 85% of the sites, greater than 0·85 (Kennedy, 1995). For the mean number of species/eel, mean number of parasites/

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eel, and mean Brillouin's Index, there were significant differences among regions ($P < 0{\cdot}0001$), with Australia ($n = 10$) being higher than Nova Scotia ($n = 24$) and the United Kingdom ($n = 14$).

In eels from Nova Scotia, the proportion of eels with 0–1 species was greater than 0·9 in 84% of the sites, the lowest proportion being 0·77 (see Appendix 3). Among UK sites, the lowest proportion of eel intestinal infracommunities with 0–1 species was 0·61, and usually at least 75% of the infracommunities possessed 0–1 species (Kennedy, 1993, 1995; Kennedy *et al*. 1986). In Australia, the proportion of eel intestinal infracommunities with only 0–1 species was less than 0·3 at 80% of the sites (Kennedy, 1995). Infection parameters for intestinal infracommunities of eels at individual sites in Nova Scotia are presented in Appendix 3.

Specialists and generalists

In fresh water, 7 species of parasite of a total of 12 (see Marcogliese & Cone, 1996) in Nova Scotia were specialists in eels. These included *Pseudodactylogyrus anguillae*, *Crepidostomum brevivitellum*, *Bothriocephalus claviceps*, *Proteocephalus macrocephalus*, *Daniconema anguillae*, *Paraquimperia tenerrima* and *Ergasilus celestis*. Eight specialists of a total of 25 species occurred in eels from freshwater in the UK. These included *Pseudodactylogyrus bini*, *P. anguilla*, *B. claviceps*, *P. macrocephalus*, *P. tenerrima*, *Spinitectus inermis*, *Anguillicola crassus* and *Ergasilus gibbus* (Kennedy, 1974, 1990; Esch *et al*, 1988; Kennedy & Fitch, 1990; Nie & Kennedy, 1991). In Australia, at least 15 of 27 species found were specialists, with 7 generalists, the rest being of unknown categorization (Kennedy, 1995).

Specialists were dominant in Nova Scotian total component communities, with only 3 exceptions (see Appendix 1). Among total component communities in Australian eels, specialists were dominant except for 2 species of unknown affiliation, which may indeed be specialists (Kennedy, 1995). In total component communities from the British Isles, specialists were dominant in 5 of 12 systems (Esch *et al*. 1988).

DISCUSSION

The present study sheds light on differences in the structure of eel parasite communities from either side of the Atlantic. Eels from the UK and Nova Scotia are infected with a similar number of specialist parasites, 5 of which are shared or closely related, being *P. anguilla*, *B. claviceps*, *P. macrocephalus*, *P. tenerrima* and *Ergasilus* spp. (Marcogliese & Cone, 1993). In Nova Scotia, the specialists are almost always dominant, whereas they are dominant in about 40% of the systems in the UK (Esch *et al*. 1988; Kennedy, 1990). These facts imply that there is a substantial phylogenetic component to parasite community structure in eels from the UK and Nova Scotia, which is shared between the 2 regions. Similarity of Atlantic eels with *A. reinhardtii* in terms of species composition of specialists is limited, with species of *Pseudodactylogyrus*, *Bothriocephalus*, *Spinitectus* and *Anguillicola* (which is an introduction in Europe) occurring in Australia (Kennedy, 1995). The close similarity and potential shared historical influence on parasite community structure in *A. rostrata* and *A. anguilla* may not be unexpected given that these 2 species are considered sister species, more recently associated with each other than with eels from the Pacific (Avise *et al*. 1986, 1990; Marcogliese & Cone, 1993). Evidently, the ancestral eel population in the Atlantic contained a parasite community not that dissimilar in membership to those in the American and European eels today (Marcogliese & Cone, 1993). Given that so many specialists occur in eels in Australia, and that they occur as dominant species, it appears that there is a phylogenetic component contributing to the diverse parasite community structure there also, with limited similarity to that in eels from the North Atlantic. A phylogenetic component influencing parasite community structure is characteristic of hosts in their heartlands (Kennedy & Bush, 1994).

The presence and acquisition of generalist parasites greatly influenced community composition of eel parasites in all 3 regions (Kennedy, 1990, 1995). Availability of generalist parasites is dependent on the local presence of other hosts and is indicative of supply-side ecological processes (Kennedy & Bush, 1994). Clearly the differences in species composition of generalists among the regions is a reflection of the differences in species composition of other fish species among those areas. In addition, the higher number of species of eel parasites occurring in the British Isles ($n = 25$) compared to Nova Scotia ($n = 12$) (Kennedy, 1974, 1990; Esch *et al*. 1988; Marcogliese & Cone, 1996) may be related to the number of other fish hosts present, with 52 in the UK versus 33 in Nova Scotia (Scott & Crossman, 1973; Maitland & Campbell, 1992), from which generalist parasites are acquired. Barker, Marcogliese & Cone (1996) demonstrated that, beyond the watershed scale, species richness of eels in North America increased with geographical range, which was a result of accumulation of generalist parasites acquired from other host species. A similar phenomenon occurs in Europe, as species richness of eel parasites increases as host range expands with the addition of new species (Moravec, 1985; Køie, 1988; Orecka-Grabda & Wierzbicka, 1994). While the species composition of eel parasites in any one locality (within-region variation) is partly a result of local processes which determine the local composition of other fish host species, the large-scale differences in species composition among the regions

(among-region variation) are a result of biogeographical and evolutionary regional processes which determine continental biotas.

Development of eel parasite communities in Nova Scotia and the British Isles has proceeded in slightly different directions since their divergence after the last glaciation. While all measurements of parasite community structure at both host individual- and population-level scales are statistically indistinguishable, the membership has changed. The influence of host-specific parasites is much greater in Nova Scotia than in the UK, whereas generalist parasites acquired from other host species are more numerous and usually dominant in Britain.

Although there was no statistically significant difference between Nova Scotian and British eels for any of the measures of parasite community structure, one cannot help but notice that in every case mean values are lower in Nova Scotia than in the UK. Marcogliese & Cone (1996) have examined the distribution of eel parasites across Nova Scotia and have demonstrated that diversity is lower in acidified systems, which are abundant in Nova Scotia. The consistently lower mean values of these measures in American eels are a result of widespread acidification of rivers. For example, species richness and diversity were higher in eels from streams of $pH > 5{\cdot}4$ compared to streams of $pH < 5{\cdot}4$ (Marcogliese & Cone, 1996). Thus, it appears that only subtle changes have taken place in parasite community structure of eels in Nova Scotia and the UK since glaciation. We suspect that significant changes in Nova Scotia occurring in the last few decades as a result of anthropogenic acidification are currently underway. If true, it is interesting that the membership of the community is being influenced differentially, and involves loss primarily of generalists and, to a lesser extent, the specialists (see Marcogliese & Cone, 1996).

Virtually every measure of parasite species richness and diversity was significantly higher in Australian eels than in eels from Nova Scotia and the UK. This pattern applies across scales, whether considering total component communities, intestinal component communities, or intestinal infracommunities. Rohde *et al*. (1995) revealed that measures of ectoparasite diversity and abundance in fishes were positively correlated with mean temperature range occupied by the host. Some factor related to temperature and latitude, whether it be increased host feeding rates (Kennedy, 1995) or increased evolutionary rates (speciation) (Rohde, 1992), or factors related to time spent in a region (Guégan & Kennedy, 1993), could explain the differences in parasite diversity and richness observed between tropical Australian eels and the boreal Atlantic eels. However, the mean temperature range experienced in Nova Scotia is 10 °C higher than that in the UK due to the colder winters experienced on the west side of the Atlantic Ocean (Critchfield, 1966), yet the diversity of eel parasites is similar on both sides of the Atlantic. This temperature difference may not be sufficient detectably to influence parasite community structure in eels. Thus, as reported by Kennedy (1995), it is impossible to distinguish between the time hypothesis and the latitude hypothesis as a causal explanation, because Nova Scotia does not differ in latitude (or temperature) a great deal from the British Isles, and eel populations from the 2 regions are the same age historically.

Alternatively, similarity between the parasite community structure of eels from Nova Scotia and the United Kingdom may be a result of saturation, that is, a limit to the number of niches in both host species, as proposed for European eels (Kennedy & Guégan, 1996). However, Kennedy (1995) suggested that certain niches in European eels were empty in comparison to Australian eels, and the same appears to apply in American eels. Despite the recent contention that European eel parasite infracommunities are saturated (Kennedy & Guégan, 1996), the persistence of empty niches in Nova Scotia is supported by the reduction in parasite diversity with acidification and subsequent recolonization observed after liming in Nova Scotia (Cone, Marcogliese & Watt, 1993; Marcogliese & Cone, 1996). Certainly the much higher species richness, diversity and parasite numbers at all levels of community organization of Australian eels demonstrate that Atlantic eels can probably be host to many more parasites, at least at the component community level. In evolutionary terms (*sensu* Wilson, 1969), the Atlantic eel communities could be considered in the non-interactive phase, where an equilibrium between rates of colonization and rates of extinction has not been attained (see Holmes & Price, 1986).

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APPENDIX 1. Richness characteristics of the total component communities of macroparasites of eels (*Anguilla rostrata*) in Nova Scotia

Locality	Total no. of species	Mean no. of species/eel (±S.D.)	Mean no. of parasites/eel (±S.D.)	No. of allogenic spp.	Proportion of autogenic individuals	Berger–Parker Index	Nature of dominant sp.	Identity of dominant sp.*
Gold R. 1989	4	0·40±0·67	1·9±5·7	0	1·00	0·77	Auto	*Para*
Gold R. 1990	3	0·20±0·41	0·6±1·3	1	0·94	0·71	Auto	*Para*
East R. (Chester) 1989	3	0·70±0·47	3·0±4·9	1	0·99	0·57	Auto	*Para*
East R. (Chester) 1990	2	0·26±0·52	0·8±3·0	0	1·00	0·92	Auto	*Para*
East R. (Chester) 1991	2	0·37±0·49	1·8±3·6	0	1·00	0·93	Auto	*Para*
Canaan R. 1989	3	0·67±0·48	1·5±1·7	0	1·00	0·93	Auto	*Para*
Canaan R. 1990	1	0·10±0·31	0·2±0·7	0	1·00	1·00	Auto	*Para*
Canaan R. 1991	4	0·63±0·61	3·6±5·6	0	1·00	0·84	Auto	*Para*
Bad Lake Run 1989	2	0·38±0·49	0·6±1·1	0	1·00	0·65	Auto	*Para*
Bad Lake Run 1990	6	0·70±0·88	3·8±7·4	1	0·99	0·68	Auto	*Erg*
Bad Lake Run 1991	6	0·60±0·81	1·9±3·6	0	1·00	0·62	Auto	*Para*
Tangier R. 1989	5	0·70±1·09	2·7±4·4	1	0·99	0·62	Auto	*Para*
Tangier R. 1990	2	0·10±0·31	0·2±0·7	0	1·00	0·83	Auto	*Erg*
East R. (St Margarets) 1989	2	0·43±0·50	0·7±1·0	0	1·00	0·91	Auto	*Para*
East R (St Margarets) 1990	4	1·00±0·59	8·4±13·1	0	1·00	0·8	Auto	*Para*
Middle R. 1989	1	0·52±0·51	1·2±1·4	0	1·00	1·00	Auto	*Para*
Middle R. 1990	2	0·48±0·57	1·4±2·2	0	1·00	0·98	Auto	*Para*
Schubenacadie R. 1980	4	1·00±1·55	10·5±19·9	0	1·00	0·9	Auto	*Pomph*
Partridge R. 1989	3	0·20±0·41	0·7±2·4	1	0·95	0·77	Auto	*Para*
Partridge R. 1990	1	0·13±0·35	0·1±0·3	0	1·00	1·00	Auto	*Para*
Vinegar Lake 1990	6	1·12±0·86	8·4±17·0	0	1·00	0·46	Auto	*Para*
Ingram R. 1990	5	1·33±0·66	4·7±3·4	0	1·00	0·84	Auto	*Para*
Nine Mile R. (Timberlea) 1990	2	0·57±0·57	1·6±2·9	0	1·00	0·98	Auto	*Para*
Martins R. 1990	1	0·62±0·49	2·7±3·5	0	1·00	1·00	Auto	*Para*
Vaughns R. 1990	2	0·97±0·56	4·0±4·5	0	1·00	0·93	Auto	*Para*
Mersey R. 1990	5	0·69±0·97	2·5±4·8	0	1·00	0·45	Auto	*E. lat*
Mushamush R. 1990	5	0·80±0·76	2·1±3·1	1	0·98	0·6	Auto	*Azygia*
Quarks R. 1990	1	0·38±0·49	0·5±0·8	0	1·00	1·00	Auto	*Para*
Nine Mile R. 1992	4	0·46±0·78	8·9±22·5	0	1·00	0·91	Auto	*Crep*
Nine Mile R. 1993	7	1·33±1·06	7·0±9·3	1	0·98	0·64	Auto	*Crep*
Nictaux R. 1992	4	0·45±0·57	1·3±3·1	0	1·00	0·62	Auto	*Erg*
St Mary's R. 1993	2	0·27±0·52	0·7±1·6	0	1·00	0·95	Auto	*Para*
Clyde R. 1993	4	0·40±0·50	0·8±1·4	0	1·00	0·8	Auto	*Para*
Tusket R. 1991	5	0·47±0·57	1·8±5·3	0	1·00	0·64	Auto	*Erg*
Stewiache R. 1993	4	0·87±0·68	2·9±4·5	0	1·00	0·71	Auto	*Para*
Roseway R. 1993	2	0·93±0·59	2·6±2·6	0	1·00	0·85	Auto	*Para*

* *Para*, *Paraquimperia tenerrima*; *Erg*, *Ergasilus celestis*; *Pomph*, *Pomphorhynchus bulbocolli*; *E. lat*, *Echinorhynchus lateralis*; *Azygia*, *Azygia longa*; *Crep*, *Crepidostomum brevivitellum*.

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APPENDIX 2. Richness and diversity characteristics of the intestinal component communities of helminths of eels (*Anguilla rostrata*) in Nova Scotia

Locality	Total no. of species	Eels infected (%)	Simpson's Index	Shannon–Wiener Index	Berger–Parker Index	Dominant species
Gold R. 1989	3	23·3	1·52	0·6	0·8	Nem
Gold R. 1990	2	16·7	1·67	0·56	0·75	Nem
East R. (Chester) 1989	1	60·0	1·00	0	1	Nem
East R. (Chester) 1990	2	23·3	1·18	0·28	0·92	Nem
East R. (Chester) 1991	2	36·7	1·16	0·26	0·93	Nem
Canaan R. 1989	2	63·3	1·1	0·18	0·96	Nem
Canaan R. 1990	1	10·0	1·00	0	1	Nem
Canaan R. 1991	3	56·7	1·11	0·23	0·95	Nem
Bad Lake Run 1989	1	20·7	1·00	0	1	Nem
Bad Lake Run 1990	3	36·7	2·28	0·93	0·63	Nem
Bad Lake Run 1991	4	43·3	1·79	0·85	0·73	Nem
Tangier R. 1989	3	23·3	2·33	0·88	0·52	Nem
Tangier R. 1990	1	3·4	1·00	0	1	Nem
East R. (St Margarets) 1989	2	43·3	1·21	0·3	0·91	Nem
East R. (St Margarets) 1990	3	83·3	1·03	0·09	0·99	Nem
Middle R. 1989	1	51·7	1·00	0	1	Nem
Middle R. 1990	2	44·8	1·05	0·11	0·98	Nem
Schubenacadie R. 1980	4	50·0	1·22	0·41	0·9	Acanth
Partridge R. 1989	1	10·0	1·00	0	1	Nem
Partridge R. 1990	1	13·3	1·00	0	1	Nem
Vinegar Lake 1990	5	73·1	2·48	1·05	0·47	Nem
Ingram R. 1990	4	93·3	1·39	0·59	0·84	Nem
Nine Mile R (Timberlea) 1990	1	53·3	1·00	0	1	Nem
Martins R. 1990	1	62·1	1·00	0	1	Nem
Vaughns R. 1990	1	80·0	1·00	0	1	Nem
Mersey R. 1990	4	30·8	1·88	0·85	0·71	Acanth
Mushamush R. 1990	2	30·0	2·1	0·69	0·52	Nem
Quarks R. 1990	1	37·5	1·00	0	1	Nem
Nine Mile R. 1992	2	29·2	1·02	0·06	0·99	Trem
Nine Mile R. 1993	3	70·0	1·8	0·76	0·71	Trem
Nictaux R. 1992	1	24·1	1·00	0	1	Nem
St Mary's R. 1993	2	23·3	1·11	0·2	0·95	Nem
Clyde R. 1993	3	36·7	1·44	0·57	0·83	Nem
Tusket R. 1991	4	33·3	4·38	1·35	0·32	Cest
Stewiache R. 1993	2	73·3	1·07	0·14	0·97	Nem
Roseway R. 1993	2	80·0	1·36	0·43	0·85	Nem

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APPENDIX 3. Richness and diversity characteristics of the intestinal infracommunities of helminths of eels (*Anguilla rostrata*) in Nova Scotia

Locality	Mean no. of species/eel (±S.D.)	Max. no. of species/ eel	Mean no. of worms/eel (±S.D.)	Max. no. of worms/ eel	Mean Brillouin's Index/eel (±S.D.)	Max. Brillouin's Index/eel	Proportion of samples with 0 or 1 species
Gold R. 1989	0·33±0·66	2	1·8±5·7	29	0·15±0·19	0·37	0·9
Gold R. 1990	0·17±0·38	1	0·5±1·3	5	0	0	1·00
East R. (Chester) 1989	0·60±0·50	1	1·7±2·3	10	0	0	1·00
East R. (Chester) 1990	0·26±0·52	2	0·8±3·0	16	0·05±0·13	0·35	0·97
East R. (Chester) 1991	0·37±0·49	1	1·8±3·6	16	0	0	1·00
Canaan R. 1989	0·63±0·49	1	1·5±1·7	6	0	0	1·00
Canaan R. 1990	0·10±0·31	1	0·2±0·7	3	0	0	1·00
Canaan R. 1991	0·60±0·56	2	3·4±4·3	16	0·02±0·08	0·35	0·97
Bad Lake Run 1989	0·21±0·41	1	0·4±1·0	5	0	0	1·00
Bad Lake Run 1990	0·43±0·63	2	1·6±3·5	14	0·10±0·22	0·58	0·93
Bad Lake Run 1991	0·50±0·63	2	1·6±3·1	15	0·07±0·16	0·44	0·93
Tangier R. 1989	0·33±0·71	3	1·0±2·2	7	0·16±0·28	0·6	0·93
Tangier R. 1990	0·03±0·19	1	0·03±0·2	1	0	0	1·00
East R. (St Margarets) 1989	0·43±0·50	2	0·7±1·0	4	0	0	1·00
East R (St Margarets) 1990	0·87±0·43	2	6·8±12·4	54	0·01±0·06	0·32	0·97
Middle R. 1989	0·52±0·51	1	1·2±1·4	5	0	0	1·00
Middle R. 1990	0·48±0·57	2	1·4±2·2	8	0·03±0·10	0·37	0·97
Schubenacadie R. 1980	1·00±1·55	4	10·5±19·9	50	0·27±0·46	0·8	0·83
Partridge R. 1989	0·10±0·31	1	0·6±2·4	13	0	0	1·00
Partridge R. 1990	0·13±0·35	1	0·1±0·3	1	0	0	1·00
Vinegar Lake 1990	1·08±0·84	3	8·3±17·0	87	0·18±0·25	0·76	0·69
Ingram R. 1990	1·30±0·65	3	4·7±3·4	14	0·15±0·21	0·58	0·67
Nine Mile R. (Timberlea) 1990	0·53±0·51	1	1·6±2·9	14	0	0	1·00
Martins R. 1990	0·62±0·49	1	2·7±3·5	13	0	0	1·00
Vaughns R. 1990	0·80±0·41	1	3·7±4·6	20	0	0	1·00
Mersey R. 1990	0·46±0·81	3	1·6±4·5	22	0·17±0·24	0·6	0·88
Mushamush R. 1990	0·30±0·47	1	0·7±1·7	9	0	0	1·00
Quarks R. 1990	0·38±0·49	1	0·5±0·8	3	0	0	1·00
Nine Mile R. 1992	0·38±0·65	2	8·2±22·5	100	0·04±0·09	0·23	0·92
Nine Mile R. 1993	0·90±0·71	2	6·4±8·9	28	0·13±0·20	0·51	0·77
Nictaux R. 1992	0·24±0·44	1	0·3±0·6	2	0	0	1·00
St Mary's R. 1993	0·27±0·52	2	0·7±1·6	7	0·04±0·11	0·28	0·97
Clyde R. 1993	0·37±0·49	1	0·8±1·4	5	0	0	1·00
Tusket R. 1991	0·33±0·48	1	0·6±1·1	3	0	0	1·00
Stewiache R. 1993	0·80±0·55	2	2·1±2·6	12	0·03±0·10	0·37	0·93
Roseway R. 1993	0·93±0·59	2	2·6±2·6	9	0·07±0·16	0·48	0·87

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REFERENCES

ATKINSON, T. C., BRIFFA, K. R. & COOPE, G. R. (1987). Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*, *London* **325**, 587–592.

AVISE, J. C., HELFMAN, G. S., SAUNDERS, N. C. & HALES, L. S. (1986). Mitochondrial DNA differentiation in North Atlantic eels: population genetic consequences of an unusual life-history pattern. *Proceedings of the National Academy of Sciences*, *USA* **83**, 4350–4354.

AVISE, J. C., NELSON, W. S., ARNOLD, J., KOEHN, R. K., WILLIAMS, G. C. & THORSTEINSSON, V. (1990). The evolutionary genetic status of Icelandic eels. *Evolution* **44**, 1254–1262.

BARKER, D. E., MARCOGLIESE, D. J. & CONE, D. K. (1996). On the distribution and abundance of eel parasites in Nova Scotia: local versus regional patterns. *Journal of Parasitology* **82**, 697–701.

CLIMAP PROJECT MEMBERS (1976). The surface of the ice-age earth. *Science* **191**, 1131–1137.

CONE, D. K., MARCOGLIESE, D. J. & WATT, W. D. (1993). Metazoan parasite communities of yellow eels (*Anguilla rostrata*) in acidic and limed rivers of Nova Scotia. *Canadian Journal of Zoology* **71**, 177–184.

CRITCHFIELD, H. J. (1966). *General Climatology*, 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

ESCH, G. W., KENNEDY, C. R., BUSH, A. O. & AHO, J. M. (1988). Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology* **96**, 519–532.

GUÉGAN, J.-F. & KENNEDY, C. R. (1993). Maximum local helminth parasite community richness in British freshwater fish: a test of the colonization time hypothesis. *Parasitology* **106**, 91–100.

HOLMES, J. & PRICE, P. W. (1986). Communities of parasites. In *Community Ecology : Pattern and Process* (ed. Anderson, D. J. & Kikkawa, J.), pp. 187–213. Blackwell Scientific Publications, Oxford.

KENNEDY, C. R. (1974). A checklist of British and Irish freshwater fish parasites with notes on their distribution. *Journal of Fish Biology* **6**, 613–644.

KENNEDY, C. R. (1990). Helminth communities in freshwater fish: structured communities or stochastic assemblages? In *Parasite Communities : Patterns and Processes* (ed. Esch, G. W., Bush, A. O. & Aho, J. M.), pp. 131–156. Chapman and Hall, London.

KENNEDY, C. R. (1993). The dynamics of intestinal helminth communities in eels *Anguilla anguilla* in a small stream: long-term changes in richness and structure. *Parasitology* **107**, 71–78.

KENNEDY, C. R. (1995). Richness and diversity of macroparasite communities in tropical eels *Anguilla reinhardtii* in Queensland, Australia. *Parasitology* **111**, 233–245.

KENNEDY, C. R. & BUSH, A. O. (1994). The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**, 187–196.

KENNEDY, C. R., BUSH, A. O. & AHO, J. M. (1986). Patterns in helminth communities: why are birds and fish different? *Parasitology* **93**, 205–215.

KENNEDY, C. R. & FITCH, D. J. (1990). Colonization, larval survival and epidemiology of the nematode *Anguillicola crassus*, parasitic in the eel, *Anguilla anguilla*, in Britain. *Journal of Fish Biology* **36**, 117–131.

KENNEDY, C. R. & GUÉGAN, J.-F. (1996). The number of niches in intestinal helminth communities of *Anguilla anguilla*: are there enough spaces for parasites? *Parasitology* **113**, 293–302.

KØIE, M. (1988). Parasites in European eel *Anguilla anguilla* (L.) from Danish freshwater, brackish and marine localities. *Ophelia* **29**, 93–118.

MAGURRAN, A. E. (1988). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton.

MAITLAND, P. S. & CAMPBELL, R. N. (1992). *Freshwater Fishes of the British Isles*. HarperCollins Publishers, London.

MARCOGLIESE, D. J. & CONE, D. K. (1993). What metazoan parasites tell us about the evolution of American and European eels. *Evolution* **47**, 1632–1635.

MARCOGLIESE, D. J. & CONE, D. K. (1996). On the distribution and abundance of eel parasites in Nova Scotia: influence of pH. *Journal of Parasitology* **82**, 389–399.

MARGOLIS, L. & ARTHUR, J. R. (1979). *Synopsis of the Parasites of Fishes of Canada*. Bulletin of the Fisheries Research Board of Canada No. 199.

MORAVEC, F. (1985). Occurrence of endoparasitic helminths in eels (*Anguilla anguilla*, (L.)) from the Màcha Lake fishpond system, Czechoslovakia. *Folia Parasitologica* **32**, 113–125.

NIE, P. & KENNEDY, C. R. (1991). Occurrence and seasonal dynamics of *Pseudodactylogyrus anguillae* (Yin & Sproston) (Monogenea) in eel, *Anguilla anguilla* (L.), in England. *Journal of Fish Biology* **39**, 897–900.

ORECKA-GRABDA, T. & WIERZBICKA, J. (1994). Metazoan parasites of the eel, *Anguilla anguilla* (L.) in the Szczecin Lagoon and River Odra mouth area. *Acta Ichthyologica et Piscatoria* **24**, 13–19.

PIELOU, E. C. (1979). *Biogeography*. John Wiley & Sons, New York.

PIELOU, E. C. (1991). *After the Ice Age : The Return of Life to Glaciated North America*. University of Chicago Press, Chicago.

ROHDE, K. (1984). Zoogeography of marine parasites. *Helgoländer Meeresuntersuchungen* **37**, 35–52.

ROHDE, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.

ROHDE, K., HAYWARD, C. & HEAP, M. (1995). Aspects of the ecology of metazoan ectoparasites of marine fishes. *International Journal for Parasitology* **25**, 945–970.

ROSNER, B. (1990). *Fundamentals of Biostatistics*, 3rd edn. PWS–Kent Publishing Company, Boston.

SCHLUTER, D. & RICKLEFS, R. E. (1994). Convergence and the regional component of species diversity. In *Species Diversity in Ecological Communities* (ed. Ricklefs, R. E. & Schluter, D.), pp. 230–240. University of Chicago Press, Chicago.

SCOTT, W. B. & CROSSMAN, E. J. (1973). *Freshwater Fishes of Canada*. Fisheries Research Board of Canada, Ottawa.

WILSON, E. O. (1969). The species equilibrium. *Brookhaven Symposia in Biology* **22**, 38–47.