

# Pattern and process in the ecological biogeography of European freshwater fish

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## Summary

1. Species lists for regions of Europe defined by Illies (1978, *Limnofauna Europaea*, 2nd edn. Gustav Fischer Verlag, Stuttgart), and augmented by information from Maitland (2000, *Guide to Freshwater Fish of Britain and Europe*. Hamlyn, London), are used to describe patterns in freshwater fish species richness and to examine the contribution of habitat preference, migration, body size and glacial history to these patterns.

2. The number of non-endemic species declines to the north and west, with increasing distance from the Ponto-Caspian region, the main source area, whereas endemic species richness declines only with latitude.

3. Habitat generalists tend to be migratory while riverine specialists are usually resident. Similar numbers of riverine species and generalists occur in Europe as a whole but generalists dominate in regional faunas and, to an increasing extent, in more isolated, formerly glaciated areas. Very few lacustrine specialists were found, reflecting the geologically ephemeral nature of lakes. Only 8% of riverine species have colonized glaciated areas, compared with more than half the generalist species, and the number declines rapidly with increasing distance from the source area.

4. Diadromous species show no geographical variation in species richness but potamodromous and resident species are affected by glaciation and by mountain and marine barriers.

5. The mean body size of regional faunas increases with latitude because there are relatively fewer small species in more distant, glaciated areas.

6. About half the species occurring in Europe are restricted to one region and the majority of these endemics occur in barrier regions with Mediterranean climates. Species in glaciated regions have much larger range sizes. Habitat preference and migration type, not body size, are the main determinants of range size.

7. Freshwater habitat availability varies across Europe with glaciated areas having more lakes of a given size than unglaciated areas. Catchment size is greatest at mid-latitudes. For a given catchment size rivers in glaciated areas are shorter.

8. The results support the notion that habitat variability, on both short and long time scales, favours colonization ability, which requires large body size.

9. As a result of their limited vagility northern fish faunas are depauperate, show high levels of plasticity and polymorphism and may show elevated speciation rates. The isolated southern faunas of the Iberian and Italian peninsulas and the Balkans are rich in endemic species but may be subject to extinctions because of the spread of the highly seasonal Mediterranean climate.

*Key-words:* body size, colonization, diadromy, glaciation, habitat availability, habitat preference, potamodromy.

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## Introduction

Over the last two decades the importance of regional processes in determining local species richness has become apparent (Ricklefs & Schluter 1993). Tonn *et al.* (1990) suggested that at the regional scale factors such

as barriers and glaciation events are likely to determine species richness and that species that overcome such factors are subject, at a more local scale, to abiotic and biotic influences. Regional, i.e. historical, processes should become more apparent as vagility decreases. Many of the ecological hypotheses proposed to explain variation in species richness invoke spatial and temporal variation in environmental conditions (Huston 1994; Brown & Lomolino 1998). Southwood (1977, 1988) argued that habitat variation in ecological time and space imposes constraints on the ecological characteristics of species. For example, species cope with fluctuating environments by being generalists or by avoiding unfavourable conditions, either through inactivity, e.g. diapause, or movement, e.g. migration. Dynesius & Jansson (2000; Jansson & Dynesius 2002) examined habitat variation on a much longer, historical, time scale. They also concluded that climatic variation selected for vagility and generalism. Generalists consuming widespread resources will have large range sizes and this and their vagility will result in increased rates of gene flow with reduced rates of speciation and extinction (though vicariant events may become more frequent).

Schlosser (1987) presented a model of stream fish assemblages based on habitat stability and biotic interactions. Greater flow variation and harsh winter conditions in headwater habitats favours small species with high reproductive rates and good colonizing ability while in the more favourable conditions and greater habitat heterogeneity found in the lower reaches biotic interactions are more important. Consistent with this, Poff & Allan (1995), Oberdorff, Huguency & Vigneron (2001) and Cattaneo (2005) showed that flow variability influenced the functional organization of fish assemblages and/or demonstrated effects on species richness. On a longer time scale, the high levels of endemism in ancient lakes have been attributed to the longer periods of time available for speciation in such habitats compared with most lakes which have lifetimes of less than 20 000 years (Russell-Hunter 1978; Cohen & Johnston 1987).

The historical biogeography of the European freshwater fauna is reasonably well known (Banarescu 1991). In the Neogene much of southern and central Europe was covered by seas: this area was subsequently recolonized from the north and east (Bianco 1990; Economidis & Banarescu 1991). However, between 115 000 and 10 000 years BP the northern European fauna was eliminated by successive glaciations (Andersen & Borns 1994). The biogeographical evidence indicates that these glaciated areas were recolonized mainly from the Ponto-Caspian region, and particularly from the middle and lower sections of the Danube basin. This conclusion has been supported by recent phylogeographical studies (see, for example Durand, Persat & Bouvet 1999; Nesbø *et al.* 1999; Bernatchez 2001; Kontula & Väinölä 2001; Kotlik & Berrebi 2001; Koskinen *et al.* 2002). Post-glacial expansions of fish from Iberia and the Adriatic were prevented by mountain ranges (Pyrenees, Alps, Dinarides, Stara Planina) and these isolated southern faunas are

faunistically much more disparate than those to the north.

Freshwater fish are ideal for examining the role of ecological factors in regional biogeography. Many species have low vagility because they are not migratory and are confined to freshwater, e.g. cyprinid fishes, whereas others are migratory and can live in the sea, e.g. salmonids. Some species are cold or warm water stenotherms and some are stenotopic, being limited to flowing or to still waters. The relative importance of such characteristics in recolonization following the extensive glaciations that covered much of Europe should be reflected by regional differences in species composition. This paper asks what determines the distribution and species richness of European freshwater fish faunas, by examining ecological patterns at the regional scale. In particular, I consider the roles of habitat preference, migratory ability and body size in determining regional scale patterns following the last glacial period. The emphasis is on the faunas of central and northern Europe because it is here that ecological effects on colonization ability following glaciation should be most apparent.

## Methods

Most of the analyses presented here are based on presence/absence data for native fish species in 25 different regions of Europe (Fig. 1) obtained from Illies (1978). These data were supplemented by information from Maitland (2000) when estimating total species richness but, because ecological information was not available for all 271 species listed by Maitland, most of the analyses were restricted to the 211 species for which such information was available. There is a strong regional bias to these omissions but, as discussed later, this is likely to obscure rather than enhance many of the patterns examined here. Illies' (1978) 'ecoregions' were loosely defined for a wide range of animal taxa, i.e. were not specific to fish, from spatial and ecological criteria; for example, region 4 consists of the alpine areas of France, Switzerland and Austria. While identification of regions based on criteria of relevance to fish faunas is desirable I do not believe that conclusions based on data delimited by, for example, national boundaries would differ. The Pyrenees (region 2) was omitted because its small size makes it biogeographically unrealistic for fish and because it acted as an outlier in regressions.

The taxonomy used in Illies does not always accord with that found in current works. Some species recognized by Illies are now regarded as races/subspecies and their distributions were merged. The taxonomy used here follows Maitland (2000), which is based on Kottelat (1997) but without the extreme splitting suggested, for example, for salmonids and coregonids. The analysis considers cyclostomes (lampreys) and true fishes, which spend a significant fraction of their life in freshwaters: some coastal taxa that enter freshwaters only sporadically (Moronidae, Mugilidae, Pleuronectidae, Syngnathidae) were omitted.

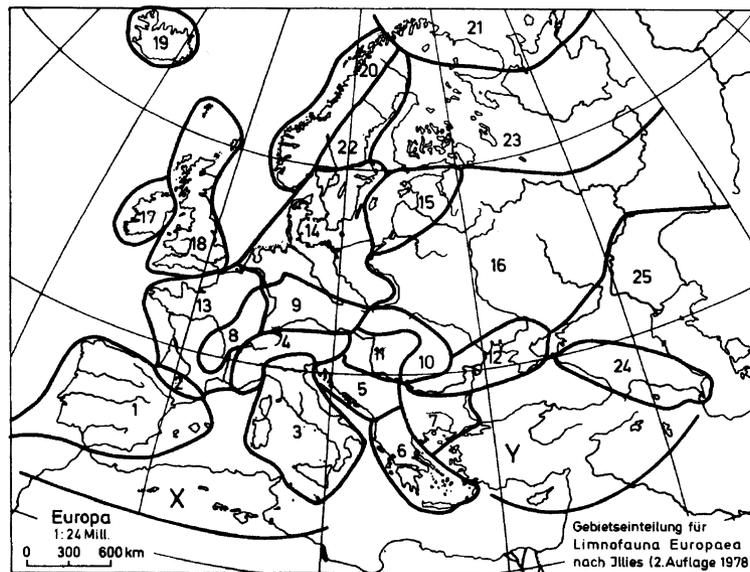


Fig. 1. Regions used by Illies (1978) (reproduced from *Limnofauna Europaea* with permission). Regions X and Y were not included in the analyses because species lists appeared to be incomplete.

A variety of sources (Ladiges & Vogt 1965; Wheeler 1969; Muus & Dahlstrom 1971; Phillips & Rix 1985; Holcik 1986; Pecl 1990; Greenhalgh 1999) were consulted for information on maximum fish lengths and habitat preferences: note that not all observations of size and habitat recorded in these books will have been made independently. Where works disagreed I placed greater emphasis on Holcik (1986), Maitland (2000) and Ladiges & Vogt (1965) and chose a value or habitat that was consistent with these or the majority of sources. Species were identified as occurring in riverine (R), lacustrine (L), generalist (RL, occurring in both habitats) or coastal (C) habitats. Regions were identified as glaciated or unglaciated depending on whether or not they were covered by ice during the last glaciation: only region 16 fell along this boundary and was omitted from the analysis when this might have affected results. In some analyses areas adjacent to glaciated regions were categorized as periglacial (regions 8–11, 13, 16).

Using information in Maitland (2000) fish were scored as plant feeders (1), invertebrate feeders (2) or piscivores (3): species consuming more than one of these categories as adults were given intermediate scores. Spawning substrates were categorized by the degree of substratum stability as stones (1), stones/plants (2), plants (3) or pelagic (4) and the degree of parental care was scored as exposed (1), hidden (2), or protected eggs/young (3).

Nikolsky (1963), McDowall (1988), Smith (1991), Cowx & Welcomme (1998) and Lucas & Baras (2001) were used to identify whether species are diadromous (migrate between sea and freshwater during their life cycle, score = 3), potamodromous (migrate within freshwaters, score = 2) or resident (species that show no more than local movements, score = 1). Some species can show more than one behaviour, e.g. charr and trout can be diadromous, or potamodromous: I identified such species as diadromous as the evidence for diadromy is more firmly established

(though see Dodson 1997), as diadromous individuals normally migrate along river channels and as such fish will experience fewer barriers to movement between regions.

The mean latitude and longitude of species was determined as the average of the latitudinal and longitudinal midpoints for each region, weighted by regional area: values will be incorrect for those species whose ranges extend outside the area covered by Illies (up to 60° east). Only 30 of the 271 species extended further east and of these 14 were predominantly northern in their distributions and only seven southern. Range area was calculated as the sum of the areas of the regions in which a species was recorded: this overestimates true range areas for species confined to Europe, particularly for those with small geographical ranges.

To test what effect distance from the source had on the probability of colonization is far from straightforward (see, for example, Olden, Jackson & Peres-Neto 2001). While most species spread from the Ponto-Caspian region and some information is emerging about colonization routes it is not known how the majority of species arrived at a particular location. In the absence of detailed information the distance travelled from the source was determined as the straight line distance between the source population (arbitrarily taken as the mouth of the Sea of Azov, the approximate midpoint of regions 7, 12, 24, 25) to the midpoint of the destination region.

Numerous analyses have shown that species richness varies with area (see references in Rosenzweig 1995). However, the analyses presented here are based on richness per region because species richness varied only weakly with regional area ( $r^2 = 0.18$ ,  $n = 24$ ,  $P = 0.04$ ) and the relation was no longer significant when the outlier (Iceland) was omitted: this region has few fish species for reasons unrelated to area.

All (fork) lengths are in mm, all logarithmic transformations are to the base 10 and, unless otherwise

**Table 1.** The percentage of variance accounted for at successive taxonomic levels for fish. The results are based on a three-level nested analysis of variance of log-transformed data. 0-values were assigned when the calculated variance component was negative; these values were always small relative to the dominant component

Group	Variable	Species	Genus	Family	Order	Source
Freshwater fish	Length	69	8	13	11	This study
	Shape	78	5	0	18	This study
	Habitat preference group	79	9	12	0	This study
Marine fishes	Length	87	0	14	0	Pauly (1980)
	Brody growth coefficient	86	0	14	0	Pauly (1980)
	Mortality rate	81	0	19	0	Pauly (1980)

**Table 2.** Effect of habitat preference on species richness across Europe, by region and by distribution group and the percentage of species recolonizing glaciated areas. No habitat information was available for two of the 211 species

	Riverine	Lacustrine	Generalist	Coastal	Total
Number of species	81	11	95	22	209
% of European species	38.8	5.3	45.5	10.5	
Mean percentage region <sup>-1</sup> ± 95% CI	19.2 ± 4.3	2.7 ± 0.8	70.8 ± 5.7	7.3 ± 2.8	
Restricted to unglaciated areas (U)	73	7	41	16	137
Restricted to glaciated areas (G)	2	3	7	0	12
Found in both areas (UG)	6	1	47	6	60
% recolonizing glaciated areas	7.6	12.5	53.4	27.3	30.5

stated, all interval estimates are standard errors and all nonlinear trend lines in the figures are fitted by locally weighted scatterplot smoothing (LOWESS). All statistical tests of percentage data were carried out on arcsine-square root transformed values though the mean percentages in the text and tables are the untransformed values. Compositional similarity of fish faunas was measured as relative euclidean distances, which were then clustered by Ward's method. Differences in proportions were tested following the procedures in Fleiss (1973).

Ideally, hypotheses in biogeography should be tested using phylogenetically independent contrasts. While phylogenies are known for some European fish taxa in others there is extreme confusion. For example, in the cyprinids, comprising 50% of the species examined in this study, the phylogeny is not clear even at subfamily level in some groups while the genus *Leuciscus* is polyphyletic (Briolay *et al.* 1998; Hänfling & Brandl 2000). Nested ANOVA was used to determine the taxonomic distribution of variance (Harvey & Pagel 1993), using a composite taxonomy based on papers by Briolay *et al.* (1998), Gilles *et al.* (1998), Hänfling & Brandl (2000) and Zaragüeta-Bagils *et al.* (2002). Most of the variance in body size and shape, the only continuously distributed variables and in habitat preference group, a discrete variable that is approximately normally distributed, occurs at the species level (Table 1). Consequently, I treated species as independent data points.

## Results

### PATTERNS IN SPECIES RICHNESS

The number of species per region is greatest in the Ponto-Caspian area and declines to the north and west

(Fig. 2a). This pattern is a composite of two patterns: the number of endemics, i.e. species found in only one region declines with increasing latitude (Fig. 2b) while non-endemic richness is greatest in the Ponto-Caspian area and declines to the west, north and south (Fig. 2c).

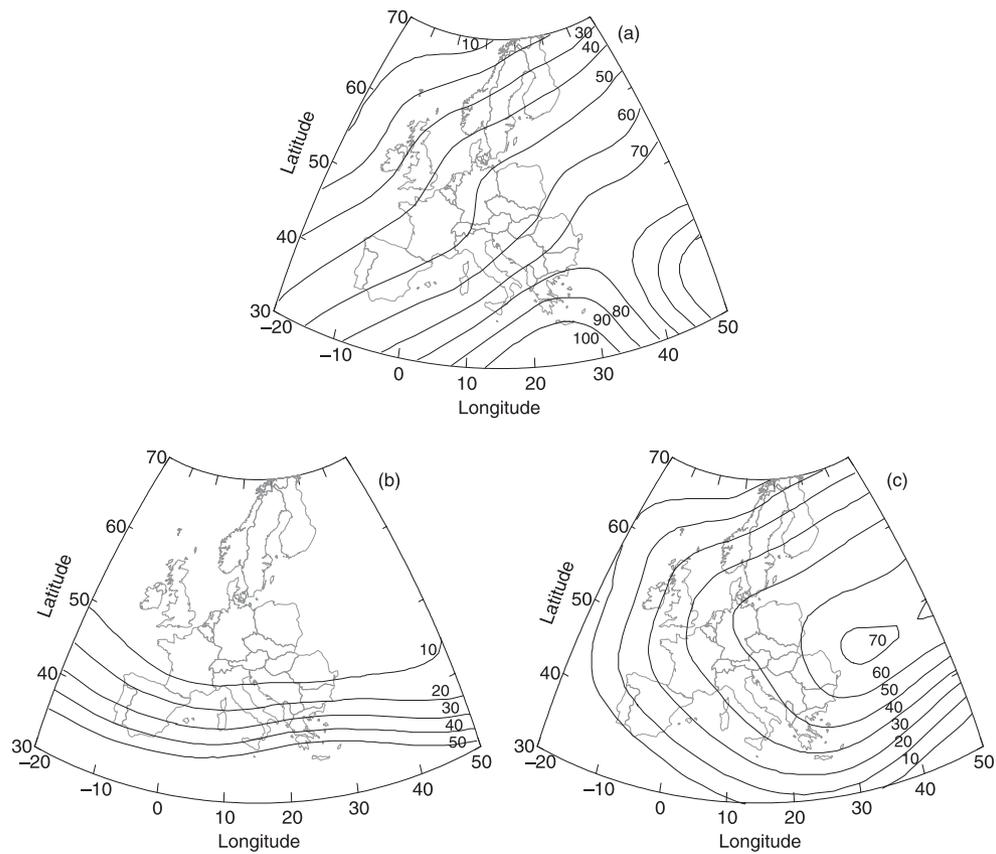
Land mass declines to the west (Fig. 3a) and possibly constrains species richness (number of species – land mass  $r = 0.77$ ,  $n = 13$ ,  $P < 0.01$ ): land mass also declines to the north (Fig. 3b) but there are additional reasons for the decline in richness with increasing latitude (see later). Note that there are appreciably more species recorded in southern Europe than expected from land mass and fewer than expected in the north.

As might be expected from Fig. 2 clustering of regions by species presence/absence produces spatially consistent clusters that differ in species richness (Fig. 4).

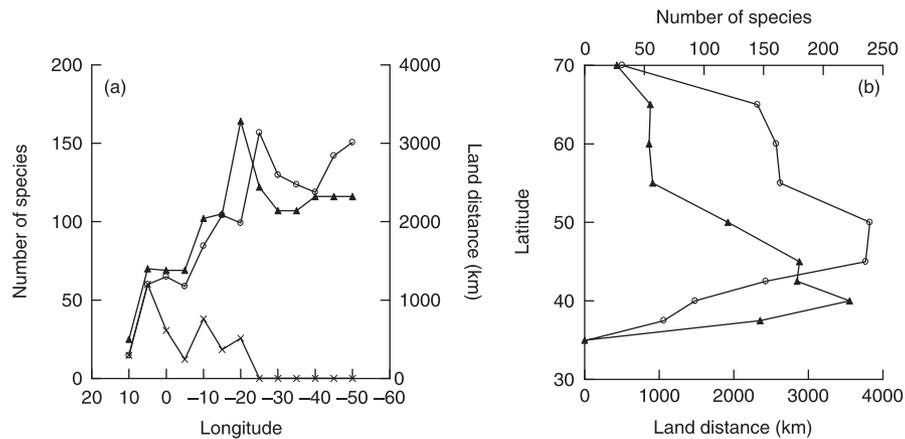
### HABITAT PREFERENCE GROUPS

While there are only slightly more generalist than riverine species in Europe as a whole, regional faunas are dominated by generalists (Table 2). Note also the scarcity of lacustrine specialists. Habitat preference group composition varies spatially (Fig. 5a): species from glaciated regions show a greater proportion of generalist and lacustrine species while riverine and coastal species (not shown) are under-represented. There are significant positive correlations across regions between riverine and coastal species richness and between generalist and lacustrine species richness ( $r = 0.74$ ,  $0.63$ , respectively;  $n = 24$ ,  $P \leq 0.001$ ) but not between other habitat combinations.

Species were classified as occurring only in unglaciated (U) or glaciated areas (G) or as widespread (found in both, UG) (Table 2). Seventy per cent ( $n = 197$ ) of the



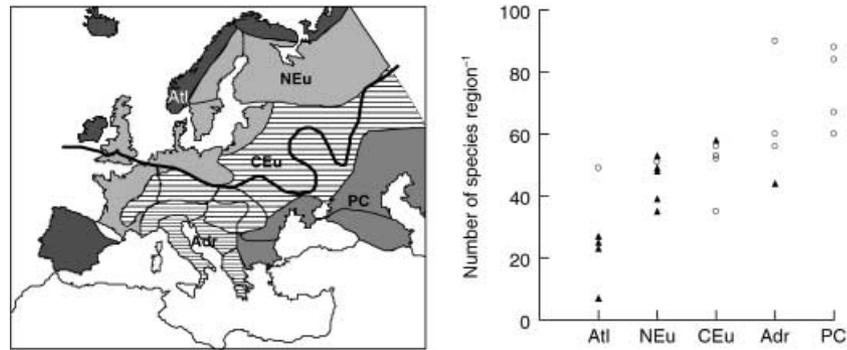
**Fig. 2.** Species richness per region varies with latitude and longitude (lines fitted by distance-weighted least squares, tension 0.5). (a) Total species richness; (b) endemic species richness; (c) non-endemic (species occurring in more than region) species richness. The number of species per region are shown on the isoclines. The plots are based on all the species recorded in a given region, including those for which there was no morphological or ecological information.



**Fig. 3.** Species richness (▲) as a function of (a) longitude and (b) latitude, and the corresponding changes in land mass (measured as distance) across all regions (○) and across barrier regions (×).

species occurring in unglaciated areas are restricted to these areas. There are important distributional differences between the habitat groups ( $\chi^2 = 37.96$ , 3 d.f.,  $P < 0.001$ ): only 8% of riverine species have extended their range following glaciation but more than half of the generalist species have done so. If the Ponto-Caspian (Fig. 4, regions 7, 12, 24, 25) is regarded as the source area the pattern is even more striking with 66% ( $n = 56$ ) of generalist Ponto-Caspian species re-colonizing glaciated

areas compared with 10% ( $n = 41$ ) of riverine species. Only 12 of 211 species are restricted to glaciated areas in Europe: one lamprey *Lethenteron camtschaticum* (Tilesius), all seven *Coregonus*, two minnows [*Eupallasa perenurus* (Pallas), *Phoxinus czekanowskii* Berg], a loach *Sabanejewia larvata* (Filippi) and a sculpin *Cottus poecilopus* Heckel. Ten of these species have distributions extending to the east of previously glaciated northern areas, suggesting that postglacial expansion occurred



**Fig. 4.** Spatial distribution (left) and species richness (right) of regional clusters. The thick line on the map shows the maximum southern extent of the ice sheet during the last 100 000 years. Richness values for unglaciated regions (○) and for glaciated regions (▲). Atl = Atlantic, NEu = North-western Europe, CEu = Central Europe, Adr = Adriatic, PC = Ponto-Caspian.

**Table 3.** Number and percentage of migratory species occurring in the various habitat preference groups and the percentage of migration group species by distribution group.  $n$  = total number of species in each group

	Riverine	Lacustrine	Generalist	Coastal	
$n$ Diadromous species	13	2	14	1	
% Diadromous	16.0	18.2	14.7	—	$\chi^2 = 0.42$ , 2 d.f., NS
$n$ Potamodromous species	7	0	22	0	
% Potamodromous	9.1	0	23.9	—	$\chi^2 = 9.47$ , 2 d.f., $P < 0.01$
$n$	81	11	95	22	

	Unglaciated	Glaciated	Widespread	$N_{\text{widespread}}$	$P_{\text{colonize}}^*$	
% Diadromous	6.8	50.0	25.0	15	0.63	$\chi^2 = 23.76$ , 2 d.f., $P < 0.001$
% Potamodromous	3.8	0	40.0	24	0.83	$\chi^2 = 46.85$ , 2 d.f., $P < 0.001$
% Resident	89.5	50.0	35.0	21	0.15	$\chi^2 = 62.70$ , 2 d.f., $P < 0.001$
$n$	139	12	60			$\chi^2 = 63.24$ , 2 d.f., $P < 0.001$

\*Number of widespread species as a proportion of unglaciated + widespread species.

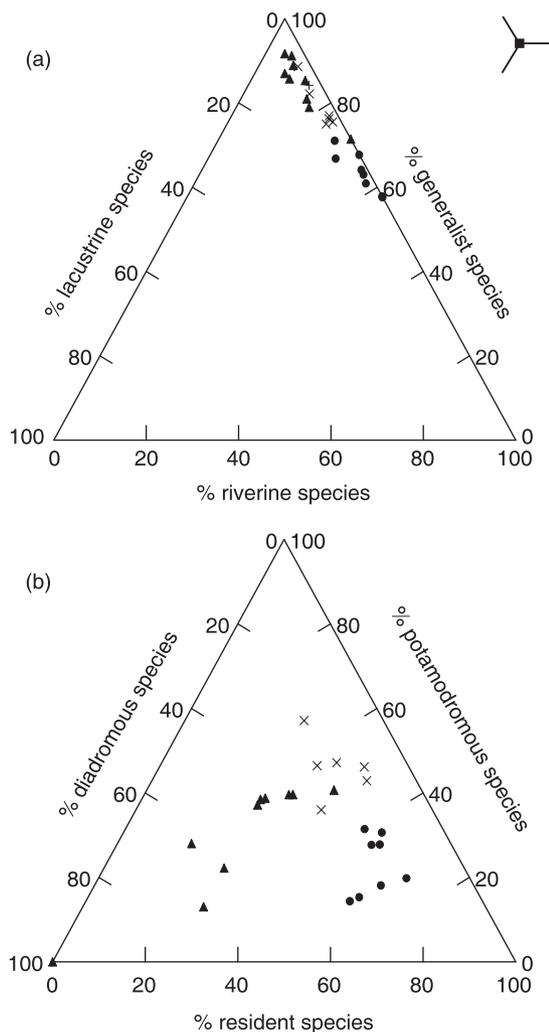
from these areas while *Sabanejewia laryata* has a very restricted alpine distribution and is considered to be a late or postglacial offshoot of *S. aurata* (Banarescu 1998). *Coregonus albula* (L.) is found predominantly in Scandinavia with only a few, scattered, populations in the Alps but it is not clear where it survived the glaciations.

#### COLONIZATION

Re-invasion of previously glaciated areas occurs because of fish movements. Habitat generalists tend to be migratory while riverine species tend to be resident ( $\chi^2 = 5.66$ , 1 d.f.,  $P < 0.05$ ). There was no significant difference in the incidence of diadromy across the various habitat preference groups but potamodromous species were more likely to be habitat generalists than exclusively riverine (Table 3). The proportions of diadromous and potamodromous species are much greater in glaciated areas (Fig. 5b) and proportionally more migratory than resident fish species are widespread (74 vs. 15%, Table 3). Note the spatial trend in Fig. 5(b). The four points to the lower right of the figure

(regions 1, 3, 5 and 6) represent unglaciated, isolated regions (see below). The next four points consist of regions in the Ponto-Caspian area, the source for most recolonization of northern Europe. As species invade periglacial regions potamodromous species become relatively more important than residents but with increasing distance from the source area diadromous species come to dominate the fauna.

Latitudinal patterns in species richness (Fig. 6a) support this interpretation. The number of resident species declines precipitously with increasing latitude ( $r = -0.72$ ,  $P < 0.001$ ) but the number of diadromous species increases slightly ( $r = 0.43$ ,  $P < 0.05$ ); the latter trend remains even when noncoastal regions are omitted. The number of potamodromous species peaks at mid-latitudes: this pattern does not depend on whether regions through which Europe's largest river, the Danube, flows (9–12) are included in parabolic regressions. The pattern reflects a significantly greater number of potamodromous species in periglacial regions than in more southern unglaciated ones ( $F_{1,14} = 11.23$ ,  $P < 0.01$ ). Diadromous species richness shows no longitudinal



**Fig. 5.** The composition of regional assemblages by glacial history and (a) habitat preference and (b) by migration category. Unglaciaded regions (●), periglacial regions (×), and glaciaded regions (▲). The insert shows the way in which coordinate values should be read. Note that the percentages in (a) do not necessarily sum to 100 because coastal species were omitted.

trend but the numbers of resident and potamodromous species per region decline from east to west ( $r = -0.53$ ,  $-0.54$ , respectively,  $n = 24$ ,  $P < 0.01$ ) (Fig. 6b). This trend is due to low species numbers in regions 17 and 19, which are islands, and on the Iberian peninsula, which is separated from the rest of Europe by the Pyrenees. These spatial differences can be summarized by the coefficients of variation (CV) across regions in migration group richness: CVs increase from 31% of the mean in diadromous species to 50% in potamodromous species and 64% in residents. Within the unglaciaded area migration category CVs are similar (32, 41, 39%, respectively) but, with the exception of diadromous species, are much greater for the glaciaded area (24, 62, 58%). Most habitat generalist species are found at mid-latitudes, whereas most riverine specialists occur in unglaciaded regions (Fig. 6c).

Some regions (1, 3, 5–7) have mountain and/or marine dispersal barriers (17–20). In unglaciaded areas

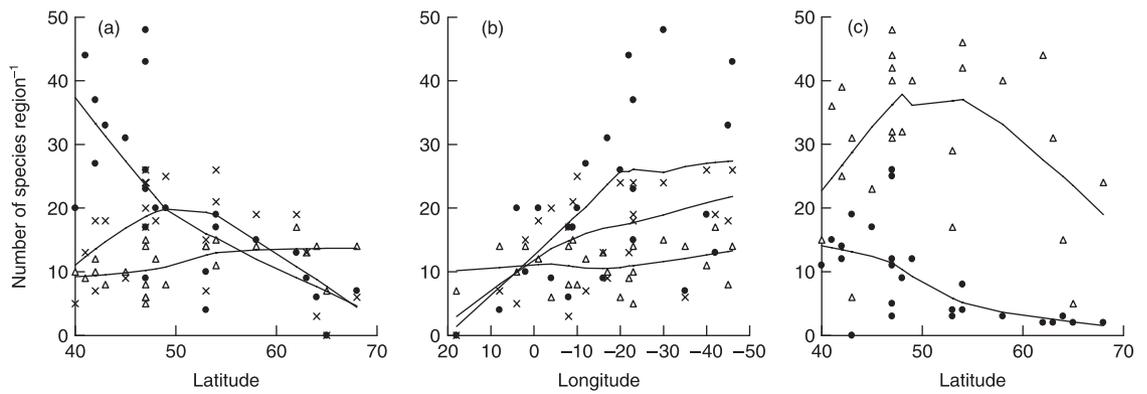
all the barriers are mountainous whereas three of the four barriers in glaciaded areas are marine. Barriers have no significant effect on total species richness in unglaciaded areas but barrier regions in glaciaded areas are impoverished (Table 4). As might be expected barriers do not affect the numbers of diadromous species per region but they do reduce the numbers of potamodromous and resident species. Note that almost all of the species found in glaciaded regions with barriers are migratory or coastal, i.e. are very likely to colonize new areas. Note also that four of the five unglaciaded barrier regions and three of four glaciaded barrier regions formed species association clusters (Fig. 4).

Species were classified as barrier sensitive, i.e. found only in barrier or nonbarrier regions, or as barrier indifferent, i.e. occurring in both barrier and nonbarrier regions. Sixty-three per cent ( $n = 63$ ) of the species found only in unglaciaded regions are barrier sensitive compared with only 5% ( $n = 61$ ) of widespread (UG) species ( $\chi^2 = 46.94$ , 1 d.f.,  $P < 0.001$ ): endemic species were excluded from this analysis and including them only increases the disparity. Hence, as expected, widespread species are better colonizers. Sixty-six per cent ( $n = 59$ ) of migratory species were widely distributed compared with only 14% ( $n = 152$ ) of resident species ( $\chi^2 = 57.10$ , 1 d.f.,  $P < 0.001$ ), reinforcing the conclusion that migratory species are less affected by barriers. Discriminant analysis of habitat preference group and migration category correctly classified 80% of nonbarrier, noncoastal species ( $n = 115$ ) by glacial distribution.

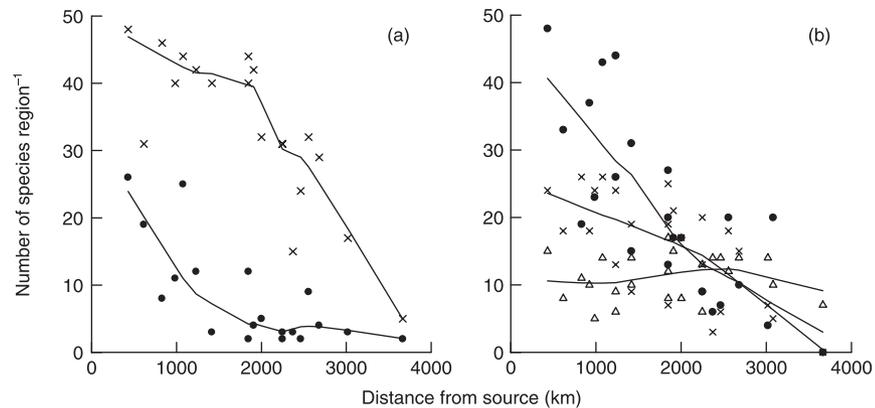
If the number of species colonizing a region is limited by vagility one would expect to find species richness differences within both habitat preference groups and migration categories with increasing distance from source. Mediterranean barrier regions were excluded from the analysis but the pattern or slopes do not change when these regions are included. Species richness is not a linear function of distance from source (significant second order terms in quadratic regressions) in habitat specialists (riverine species) or generalists (Fig. 7a) but generalist richness declines only slightly up to about 2000 km from source area whereas it is rapid in riverine species. The number of species per region should be independent of distance from source for diadromous species, as they probably colonized areas from the sea, but should decline increasingly steeply for potamodromous and resident species. These expectations are realized (Fig. 7b): slopes  $0.0003 \pm 0.0011$ ,  $P > 0.5$ ;  $-0.0072 \pm 0.0014$ ,  $P < 0.001$ ;  $-0.0123 \pm 0.0020$ ,  $P < 0.001$ , respectively.

#### BODY SIZE

Lacustrine species showed no significant size trend with latitude. The mean size of species in the other groups increased significantly with latitude, in the glaciaded regions north of  $48^\circ$  (Fig. 8), but not with longitude: the increase in mean size with latitude is much steeper for riverine and coastal than for generalist species. These



**Fig. 6.** Number of resident (●), diadromous (△) and potamodromous (×) species per region as functions of (a) latitude (b) longitude and (c) the number of riverine (●) and habitat generalist (△) species as a function of latitude.



**Fig. 7.** Number of (a) riverine (●) and generalist (×) species and (b) of resident (●), potamodromous (×) and diadromous (△) species per region as functions of distance from the Ponto-Caspian region.

**Table 4.** The effect of barriers on the mean number of diadromous, potamodromous, coastal, resident and habitat generalist species in regional faunas. *F*-values test for differences over all four categories while the probabilities test for the effect of barriers within each glaciation category

	Unglaci- ated no barriers	Unglaci- ated barriers	<i>P</i>	Glaci- ated no barriers	Glaci- ated barriers	<i>P</i>	<i>F</i> <sub>3,19</sub>
Diadromous spp.	9.3 ± 1.1	10.2 ± 1.4	NS	13.5 ± 1.3	12.3 ± 1.6	NS	2.34
Potamodromous spp.	22.4 ± 1.7	10.4 ± 2.2	< 0.001	15.8 ± 2.0	6.3 ± 2.5	< 0.01	11.73***
Coastal spp.	5.0 ± 1.3	8.8 ± 1.6	NS	2.0 ± 1.5	3.3 ± 1.8	NS	3.50*
Resident spp.	22.8 ± 2.5	23.0 ± 3.1	NS	11.0 ± 2.9	1.8 ± 3.5	0.05	10.68***
Total number of species†	59.9 ± 5.2	64.4 ± 6.6	NS	42.7 ± 6.1	23.5 ± 7.4	0.06	7.50***
% endemic species†	5.4 ± 3.2	32.8 ± 4.0	< 0.001	1.1 ± 3.7	1.0 ± 4.5	NS	17.50***
Habitat generalist spp.	38.5 ± 2.3	27.6 ± 4.4	< 0.05	35.5 ± 3.2	16.5 ± 4.9	< 0.01	7.30**
% migratory or coastal	62.6 ± 2.4	57.6 ± 3.0	NS	74.0 ± 2.7	94.6 ± 3.3	< 0.001	26.41***
<i>n</i>	8	5		6	4		

\**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001. †Calculated from complete lists based on data in Illies (1978) and Maitland (2000).

latitudinal trends are due to declines in the numbers of small species (in all habitat preference groups) but no change in the number of large species with increasing latitude (e.g. total number of species less than 30 cm  $r = -0.74$ ,  $n = 24$ ,  $P < 0.001$ ; total number of species longer than 60 cm  $r = -0.20$ ,  $P > 0.30$ ). While there were no longitudinal trends in mean size the number of both small and large species declined to the west ( $r = -0.50$ ,  $P < 0.05$ ;  $r = -0.70$ ,  $P < 0.001$ , respectively).

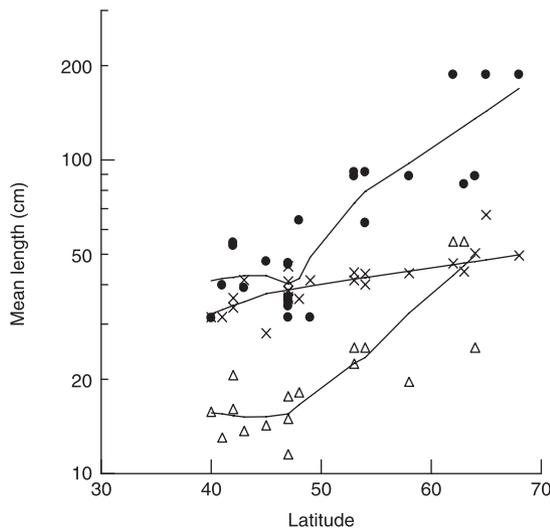
Body size varied across habitat preference groups and with migratory behaviour (Table 5) (two-way ANOVA; habitat preference groups  $F_{1,161} = 4.10$ ,  $P < 0.05$ ; migration category  $F_{2,161} = 49.19$ ,  $P < 0.001$ ; interaction  $F_{2,161} = 8.11$ ,  $P < 0.001$ ; coastal and lacustrine species omitted): diadromous species were largest and resident species smallest. Diadromous riverine species are very much larger than resident ones ( $F_{1,161} = 75.05$ ,  $P < 0.001$ ). Diadromous riverine species are also larger than

**Table 5.** Mean log lengths by habitat preference group and glacial position. The diadromous : resident length ratios for the various habitat preference groups are also shown

	Riverine	<i>n</i>	Lacustrine	<i>n</i>	Generalist	<i>n</i>	Overall	<i>n</i>
Overall mean length	1.42 ± 0.05	76	1.26 ± 0.13	10	1.50 ± 0.04	91		
Diadromous	2.20 ± 0.12	10	1.53 ± 0.02	2	1.74 ± 0.10	14	1.91 ± 0.09	26
Potamodromous	1.76 ± 0.12	7	–		1.64 ± 0.08	22	1.70 ± 0.07	29
Resident	1.24 ± 0.04	59	1.19 ± 0.15	8	1.37 ± 0.04	55	1.30 ± 0.03	122
Length ratio	9.12		2.18		2.37		4.07	
	Unglaciaded		Glaciaded		Widespread			
Overall mean length	1.32 ± 0.03	137	1.53 ± 0.09	12	1.60 ± 0.06	60		

generalists while resident riverine species are smaller ( $F_{1,161} = 11.79$ ,  $P = 0.001$ ,  $F_{1,161} = 4.18$ ,  $P < 0.05$ , respectively) but potamodromous species in the two habitat preference groups did not differ in size ( $F_{1,161} = 0.29$ ).

Species restricted to unglaciaded areas are smaller than those found only in glaciaded areas or in both areas (Table 5,  $F_{2,206} = 10.99$ ,  $P < 0.001$ ). Habitat preference group comparisons show similar patterns: the differences for riverine and generalist species are dramatic (Fig. 9)



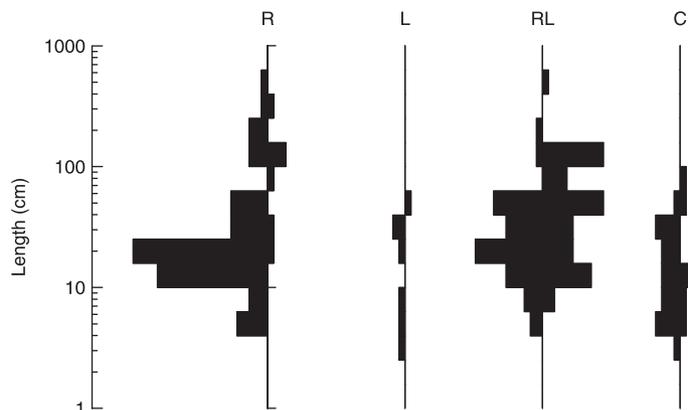
**Fig. 8.** Mean length as a function of latitude for the riverine (●), generalist (×) and coastal (△) habitat preference groups.

with species that re-invaded glaciaded areas having mean lengths 3.3 × and 1.8 × those of species that did not.

**RANGE SIZE**

The eel *Anguilla anguilla* (L.) occurs in all regions and consequently has the largest range area and a mean latitude of 51°N but range size, inevitably, declines for species with more northern or southern distributions (Fig. 10). One hundred and thirty-eight of the 271 native species listed in Maitland (2000) are endemic, i.e. confined to one region. Ninety-seven per cent ( $n = 138$ ) of endemics are found in unglaciaded areas and 79% ( $n = 134$ ) of these unglaciaded endemics occur in barrier regions and comprise, on average, one-third of the species found in these regions (Table 4). Eighty-eight per cent ( $n = 120$ ) of all species found in unglaciaded barrier regions are endemics compared with 52% ( $n = 54$ ) for nonbarrier regions ( $\chi^2 = 28.00$ , 1 d.f.,  $P < 0.001$ ). Only two of the four ‘endemics’ from glaciaded regions [*Sabanejewia larvata* and *Rutilus meidingeri* (Heckel)] are strictly limited to one region, whereas *Phoxinus czekanowskii* and *Coregonus autumnalis* (Pallas) also occur outside the study area.

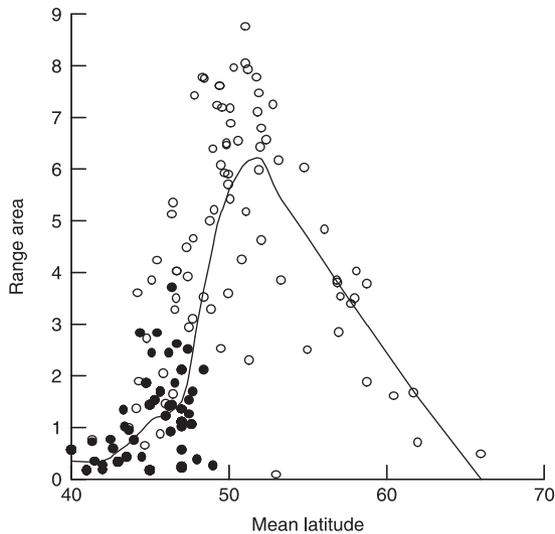
When range areas are expressed as a percentage of the maximum possible occupiable area (total unglaciaded barrier, total unglaciaded nonbarrier or all regions), marked differences become apparent between the species. As is to be expected, unglaciaded barrier species occupy the smallest proportion of their possible ranges while widespread species occupy the most (Fig. 11,



**Fig. 9.** Species size distributions for unglaciaded (left) and widespread (right) species in the various habitat groups. Mean log lengths are significantly different only for riverine (R) and generalist (RL) species ( $P < 0.01$ ).

medians for unglaciated barrier, unglaciated nonbarrier and widespread species 14, 34, 66%, respectively). Few species restricted to unglaciated regions have large ranges while few widespread species have small ranges (skewness 0.98, 0.99 and -0.47, respectively).

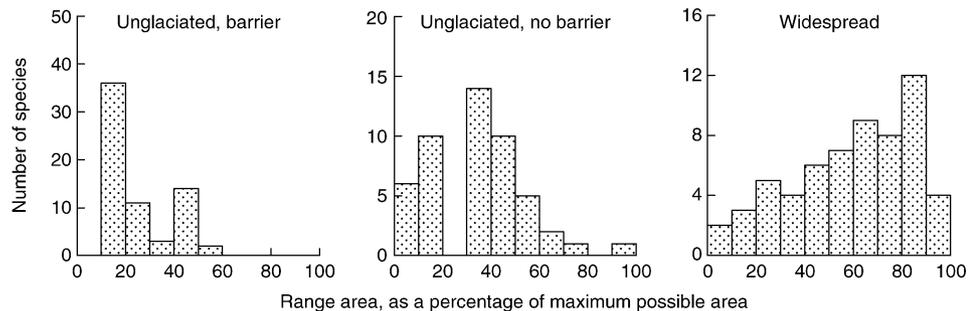
Range area varies with body size across all species ( $\log\text{-log } r = 0.35, n = 209, P < 0.001$ ) and within habitat



**Fig. 10.** Range area ( $\times 10^6 \text{ km}^2$ ) as a function of mean latitude. Species restricted to unglaciated areas are shown with filled circles. Range area, calculated as the sum of the areas of the regions in which a species was recorded, overestimates true range areas particularly for those species with small geographical ranges. Sixty species were omitted because their range area is much less than that of the region in which they occur: almost all occur south of  $45^\circ\text{N}$ .

groups ( $r_{\text{riverine}} = 0.42, n = 76, P < 0.001$ ;  $r_{\text{lacustrine}} = 0.45, n = 10, P = 0.193$ ;  $r_{\text{generalist}} = 0.30, n = 91, P < 0.01$ ). The correlation disappears when endemics are excluded from the analysis: these have smaller body sizes than more widespread species ( $F_{1,207} = 22.89, P < 0.001$ ). Migration, habitat preference group and latitude also affect range area ( $r = 0.74, P < 0.001$ ) (Table 6) but when these variables were introduced into the analysis neither body length alone nor in any interaction term contributed significantly. Residents, as expected, have smaller ranges than migratory species but, unexpectedly, potamodromous species have a mean range area significantly greater than that of diadromous species, perhaps because the latter are less likely to be found in noncoastal regions. Only generalist species had bimodal range areas (Fig. 12): most species restricted to unglaciated areas had very small ranges whereas widespread (UG) species tended to occur everywhere. While migration, habitat preference group and latitude contributed more or less equally to the predicted range size of widespread species, habitat preference was not significant for species confined to unglaciated areas and latitude was much more important than migration category ( $F_{1,103} = 0.41, F_{2,103} = 6.05, F_{1,103} = 35.02$ , respectively). The strong latitudinal effect probably reflects the decrease in land area in the southern Mediterranean area (Fig. 3b).

Within species-rich genera there were significant positive relationships between range area and body size for four taxa (*Barbus*  $r = 0.63, n = 13, P < 0.05$ ; *Chondrostoma*  $r = 0.70, n = 9, P < 0.05$ ; *Leuciscus*  $r = 0.64, n = 14, P < 0.05$ ; *Rutilus*  $r = 0.79, n = 9, P < 0.05$ ):



**Fig. 11.** Realized range area histograms for three distribution categories of fish species. Widespread species occur in glaciated and unglaciated areas and are barrier indifferent.

**Table 6.** ANOVA of log range area for species classified by habitat preference (excluding lacustrine and coastal species) and migration groups, with latitude as a covariate (total  $R^2 = 0.55$ ). All range areas within each factor are significantly different

	Mean log range area	<i>n</i>		Mean range area ( $\times 10^6 \text{ km}^2$ )
Habitat			$F_{1,164} = 4.23, P < 0.05$	
Riverine	$6.148 \pm 0.054$	77		1.40
Generalist	$6.281 \pm 0.051$	92		1.91
Migration			$F_{2,164} = 26.25, P < 0.001$	
Diadromous	$6.189 \pm 0.090$	24		1.54
Potamodromous	$6.548 \pm 0.077$	29		3.51
Resident	$5.910 \pm 0.039$	116		0.81
Latitude			$F_{1,164} = 60.12, P < 0.001$	

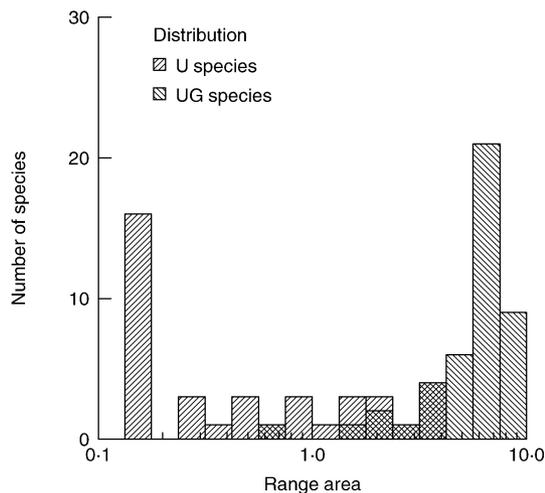


Fig. 12. Range area ( $\times 10^6 \text{ km}^2$ ) histograms for generalist species found only in unglaciated areas (U) or widespread (UG).

the data suggested an association between species number and the likelihood of detecting trends in less speciose genera. However, these significant relationships again occurred only because potamodromous species were large and had larger ranges than residents.

The area occupied by a species in the unglaciated part of its range was a good predictor of the area occupied in the glaciated part for resident and potamodromous species ( $r = 0.49$ ,  $n = 130$ ,  $P < 0.001$ ,  $r = 0.62$ ,  $n = 29$ ,  $P < 0.001$ , respectively) but there was no relationship for diadromous species ( $r = 0.23$ ,  $n = 26$ ,  $P > 0.2$ ) (Fig. 13): these patterns persist even when the unglaciated non-barrier range is used as the predictor. Only 13% ( $n = 112$ ) of species with small range areas (less than 2 million  $\text{km}^2$ ) had expanded into glaciated areas compared with 79% ( $n = 48$ ) of species with larger unglaciated ranges ( $\chi^2 = 68.07$ , 1 d.f.,  $P < 0.001$ , lacustrine and coastal species excluded). Sixty-five per cent of the species with small unglaciated ranges were riverine compared with 15% of species with larger unglaciated ranges ( $\chi^2 = 29.79$ , 1 d.f.,  $P < 0.001$ ).

#### SPECIES TRAITS AND DISTRIBUTION

The relationships between fish size, body shape (maximum depth as a proportion of body length), diet, spawning substrate and degree of parental care were investigated by principal components analysis for the 93 species for which there was sufficient data. Only the first two components had eigenvalues greater than 1.0 and these accounted for 33 and 31% of the variance, respectively. There were strong correlations between the first axis and shape, spawning substrate and degree of parental care (varimax rotated loadings 0.79, 0.60, -0.75, respectively), and between the second axis and size and diet (0.92, 0.79). There were no significant correlations between the first component and distribution but the second, size-linked, component was significantly correlated with habitat preference group

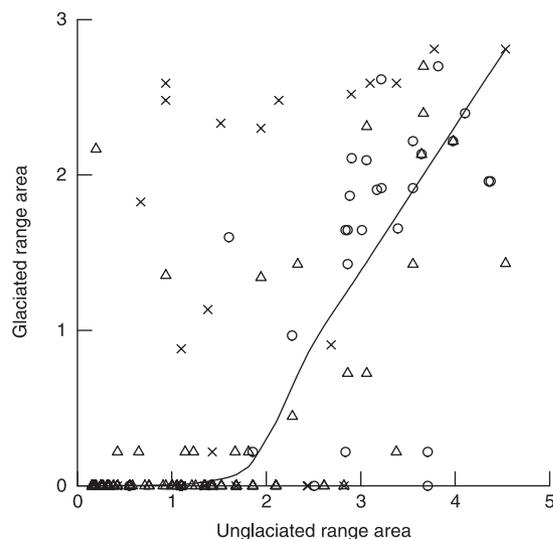


Fig. 13. The areas ( $\times 10^6 \text{ km}^2$ ) occupied by diadromous (x), potamodromous (o) and resident ( $\Delta$ ) species in the glaciated and unglaciated parts of their range: the LOWESS line was fitted to all the data points. Region 16 was omitted from the calculation of range areas because it had both glaciated and unglaciated sections.

( $r = -0.22$ ,  $P < 0.05$ ), migration category ( $r = 0.48$ ,  $P < 0.001$ ), latitude ( $r = 0.29$ ,  $P < 0.01$ ) and range area ( $r = 0.27$ ,  $P < 0.01$ ).

All purely herbivorous species were riverine and all piscivorous species were habitat generalists. Species that consume plant material occur at significantly lower latitudes than predatory species ( $F_{1,195} = 5.70$ ,  $P < 0.05$ ) and dietary scores (importance of piscivory) increased with increasing latitude ( $F_{1,195} = 4.95$ ,  $P < 0.05$ ). Diadromous fish were more piscivorous than the other two migration categories even when adjusted for differences in body size (least squares adjusted mean diet scores  $2.34 \pm 0.09$   $n = 24$ ,  $2.05 \pm 0.08$   $n = 29$ ,  $2.06 \pm 0.04$   $n = 133$  for diadromous, potamodromous and resident species, respectively,  $F_{2,182} = 4.36$ ,  $P < 0.05$ ). This difference remained even when latitude was included in the analysis, i.e. it was not because diadromous species are dominant in high latitude regions.

#### AVAILABLE HABITAT

As reported in the Methods section regional area had no effect on species richness. However, land mass is not necessarily a good guide to available habitat for aquatic species. Log transformed data (Stanners & Bourdreau 1995) show that small lakes are more numerous than large ones: the slopes do not vary with glaciation history ( $F_{1,75} = 3.13$ ,  $P = 0.08$ ) but the intercepts do and glaciated areas have 4.4 times more lakes of a given size than unglaciated areas ( $F_{1,76} = 17.63$ ,  $P < 0.001$ ).

Catchment size is ultimately constrained by land area and, as land mass declines to the west (Fig. 3), it is inevitable that maximum (and probably mean) catchment size will also decline and will be less in island (regions 17–19) and peninsula habitats (1, 3, 6, 20, 21). As

expected, catchment size does decline to the west (log catchment area – longitude  $r = 0.38$ ,  $n = 74$ ,  $P = 0.001$ ). Barriers provide further constraints. Barrier regions occur significantly to the south and west of nonbarrier regions (latitude  $F_{1,66} = 6.26$ ,  $P < 0.05$ , longitude  $F_{1,66} = 17.46$ ,  $P < 0.001$ ). Rivers in glaciated regions and in barrier regions have smaller catchments than in unglaciated and nonbarrier regions ( $F_{1,66} = 9.66$ ,  $P < 0.01$ ,  $19.74$ ,  $P < 0.001$ , respectively). Furthermore, for a given catchment area rivers are 22% shorter in glaciated areas (slopes  $F_{1,22} = 0.84$ , intercepts  $F_{1,23} = 4.47$ ,  $P < 0.05$ ). The river data presented by Stanners & Bourdreau (1995) is not a random sample but is biased towards the largest rivers in Europe: while these rivers cover more than two-thirds of Europe the majority of the smaller, missing catchments are found in Iceland, the British Isles and Scandinavia, i.e. northern, glaciated areas (Kristensen & Hansen 1994). Discharge, an indicator of potential flow conditions and therefore the type of species likely to occur, increases significantly with latitude ( $r = 0.39$ ,  $n = 28$ ,  $P < 0.05$ ): this relation is strengthened after adjusting for variation in river length ( $r = 0.50$ ,  $P < 0.01$ ).

## Discussion

### THE DATA

There are a number of potential sources of error in the data and the analyses. Some species listed by Maitland (2000) were omitted from the data set because taxonomic changes meant that the corresponding species in Illies (1978) could not be identified. Others were omitted from some analyses because there was no morphological or ecological information available. This reduced the list from 271 to 211 species. The omitted species comprise between 0 and 29% of the regional faunas and there is a southern bias: only one of the 10 glaciated regions had species omitted compared with nine of 13 unglaciated regions (mean omissions 0.5 and 7.8%, respectively). Only three of the latter regions were severely affected, with 29, 28 and 20% of species missing from regions 1, 5 and 6. The Mediterranean region is an area of high endemism (Crivelli & Maitland 1995): the omitted species have localized distributions and their omission is likely to reduce the differences described here. Again, updated knowledge of species distributions is most likely to affect southern European species with localized distributions.

The chance of a species colonizing an area depends on movement. This analysis has focused on the most obvious movement pattern, migration, but species also undergo local and seasonal and dispersal movements (Dodson 1997). The incidence of these movement types probably varies across species and environment but little is known about their importance or extent. Dodson (1997) re-classified the species identified as diadromous by McDowall (1988) and concluded that the allocations were unsubstantiated for 24% of anadromous and 42%

of catadromous species. Failure to recognize potamodromy seems particularly likely as these movements are probably smaller in extent and perhaps less likely to be detected than those of diadromous species.

Species characteristics were compiled from a number of sources but the values presented do not necessarily adequately summarize characteristics over whole species ranges as the information sources were predominantly from north-central Europe. The habitat preference groups are ill-defined, e.g. what characterizes riverine or lacustrine species other than living in rivers or lakes, and it is not known to what extent these groupings reflect abiotic preferences or exclusions due to biotic interactions, which may vary geographically.

Intraspecific variation in species characteristics has been ignored but at least some of these vary geographically. Migration tendency (McDowall 1997) can vary with latitude: for example Arctic charr *Salvelinus alpinus* (L.) and brown trout *Salmo trutta* (L.) tend to be diadromous in northern regions and resident to the south but migratory and resident individuals can occur even within a single population. However, the rather limited data available indicate that maximum body size does not vary with latitude (Belk & Houston 2002). The patterns reported here are strong enough to override any intraspecific variation in species characteristics.

The analyses have assumed that the species constitute independent data points but this is unlikely to be true (Harvey & Pagel 1993). The large amount of variance at the species level, while consistent with independently distributed species characteristics, could also be a consequence of the poor phylogenetic knowledge of the group. While some studies have found most variance is accounted for at higher taxonomic levels (Read & Harvey 1989; Smith *et al.* 2004) others have found a more or less even distribution across taxonomic levels, e.g. genome size in birds and mammals (Gregory 2002) or that most variance resides at the species level, e.g. range areas of heteropteran phytophagous hosts (Brändle, Stadler & Brandl 2000). Pauly's (1980) fish data, which do not suffer from the same level of unresolved polytomies, show a very similar pattern to the European freshwater fish data where at least two-thirds of the variance occurs at the specific level. It is too soon to say whether there are real differences between taxa or whether other factors are important in accounting for the distribution of variance. Consequently, the conclusions drawn here should be regarded as preliminary and treated with caution until the phylogeny is better documented.

### A MODEL

The results show that habitat preference, migration and body size are strongly associated with each other and with the distribution of freshwater fish in Europe. Fish move because (1) one of the habitats they occupy shows greater temporal variability than they can deal with, either because they are stenotopic and/or because the

environmental variability is extreme, or (2) there are greater net benefits in another habitat. In the long term one would expect species occupying unpredictable environments to become eurytopic, i.e. generalists. Migration is most likely to be detected when the distances moved are great, such as in large rivers, or in extreme environments, such as northern climes. Migratory species will tend to be classified as habitat generalists simply because they can be found in a variety of environments. Selection favours large size because of energetic efficiencies to migrants (Bernatchez & Dodson 1987).

This scenario predicts a more or less uniform distribution of diadromous species, geographical trends in potamodromous species attributable to variation in habitat availability and a marked decline in the number of resident species with distance from source. One would also expect migration to be most marked/frequent in stenotopic species such as salmonids and coregonids. Range size should vary with latitude and migration category. Rivers, as geologically long-lived features, would be expected to have many more habitat specialists than the relatively ephemeral majority of lakes. Migratory generalists should be widely distributed, reducing extinction rates but also speciation rates because of enhanced gene flow.

#### PHYSICAL CONSTRAINTS

The decline of non-endemic fish species richness to the north, south and west is consistent with both barrier effects and the constraints of land area. Banarescu (1991 p. 811) noted that freshwater species can be divided, by their distribution in relation to mountain barriers, into a pan-European fauna, a central European one that does not extend to the south, and several distinct southern faunas. He also pointed out that the relatively isolated southern faunas, while sharing some genera with central Europe, also have genera or lineages that are absent from there. Separating barrier and longitudinal geometric constraint effects in mainland Europe will be difficult given the position of the barrier regions. Latitudinal geometric constraints seem unlikely to be important given the considerable eastwards extension of some species into Asia, though the Ural Mountains act as a barrier for others.

However, as considered earlier, variation in land mass is not necessarily a good guide to the availability of aquatic habitat. The latitudinal and longitudinal trends in the numbers of potamodromous (Fig. 6a) and of generalist species in southern regions (Fig. 6c) parallel trends in catchment size. Baker & Ross (1981) and Pyron (1999) reported that generalists were more widely distributed than specialists while the data presented here show that habitat generalists have range areas 36% larger than those of riverine specialists (Table 6). However, Gaston & Blackburn (2000) argue that there is no relation between niche breadth and range size but that species that utilize widespread habitats (resources) are themselves widespread: Tales, Keith & Oberdorff

(2004) produce supporting evidence from riverine fish in France. If Gaston & Blackburn (2000) are correct one would expect geographical variation in river and lake habitat availability to correlate with range size. Drainage density, i.e. river length per unit area, varies considerably across Europe (Vogt *et al.* 2003) and is greatest in (mountainous) areas with high rainfall. Lakes are more abundant in glaciated areas while catchment areas are greater in unglaciated areas. However, even river features can give a misleading picture of habitat availability as streams in southern areas can dry-up or be reduced in extent in areas with low rainfall: the unglaciated barrier regions have Mediterranean climates with hot dry summers and less permanent streams (Gasith & Resh 1999; Magalhaes, Batalha & Collares-Pereira 2002). If habitat availability was the sole factor affecting species richness one would expect slightly more riverine species in unglaciated areas and many more habitat generalists and lacustrine species in glaciated regions. While the latter expectation is realized the preponderance of riverine species in unglaciated areas (Table 3) greatly exceeds any increased habitat availability. Riverine species richness is strongly correlated with catchment area (Oberdorff, Hugueny & Guégan 1997, and references therein) but I am not aware of any information on rates of species turnover across catchments in Europe.

Given the limited vagility of many fish species there is a danger of judging present day distributions in purely ecological terms. Range contractions, caused by increasing aridity, are likely to be more rapid than range expansions in freshwater fish. For example Taylor & Gotelli (1994) found evidence for smaller range sizes in arid areas in North American shiners. Mediterranean climates, with their hot, dry, summers, have expanded northwards since the last glaciation and done so more markedly in areas to the west of the Balkans (Roberts 1998). Most endemics in Europe occur in areas with Mediterranean climates, consistent with the possibility that climate-driven extinction might be an important determinant of species richness in these areas. Reynolds, Webb & Hawkins (2005) found that extinction risk in European freshwater fishes was greater for species of small body size and southern distribution: in 70% ( $n = 33$ ) of pairings the more vulnerable species was from a Mediterranean region. In addition northern Europe has probably received greater rainfall since the last glaciation (Roberts 1998): these changes are likely to have affected lake sizes and river flows.

As the glaciers retreated huge proglacial lakes formed (Segerstråle 1982; Andersen & Borns 1994). The Baltic Ice Lake, for example, covered more than 15° of longitude (Andersen & Borns 1994), allowing movement across previously isolated catchments. Segerstråle (1982), citing Grosswald (1980), shows extensive connections between the Black, Caspian and Aral Seas and northern proglacial lakes. The position of these lakes and their connections changed over time thereby providing great opportunities for dispersal (Bernatchez & Wilson 1998). Matthews (1998) notes that conditions in the lower

reaches of large, slowly flowing rivers more closely resemble those found in lakes than in headwater streams. Hence previously glaciated areas are more likely to be colonized by generalist cold water species than by riverine species. The cold water tolerance and breeding cycles of salmonids and coregonids favours their spread in glaciated areas. Proglacial lakes were likely to have been oligotrophic, i.e. well oxygenated with clear water and poor food supplies. The latter condition would be expected to favour anadromy (Gross, Coleman & McDowall 1988; McDowall 1988).

Most fishes (but not aquatic invertebrates) recolonized glaciated regions from the Ponto-Caspian region, particularly the lower and middle Danube (Banarescu 1991) and the decline in non-endemic species richness away from this region is consistent with this. Molecular phylogeographical studies have confirmed the links between Ponto-Caspian populations and the colonizers, e.g. Durand *et al.* (1999), Nesbø *et al.* (1999), Bernatchez (2001), Kontula & Väinölä (2001), Kotlik & Berrebi (2001) and Weiss *et al.* (2002), but have also shown that colonization routes were frequently far from linear, e.g. three lineages of *Cottus gobio* colonized the Baltic Sea region, from the south-west, south-east and east (Kontula & Väinölä 2001).

#### ECOLOGICAL CONSTRAINTS

Fish move for a variety of reasons (for food, breeding or to refuges) and with varying frequency (from diel to once in a life time) and extent (Lucas & Baras 2001). The extent of movement should vary with habitat predictability, the distance between alternative habitats and on the migratory capabilities of the species. Lucas and Baras adopt a broad definition of migration and point out that most migrations are not large-scale movements for breeding such as shown by some salmonids and eels. There is also considerable intraspecific variation in the occurrence, timing and extent of migrations in diadromous (Jonsson & L'Abée-Lund 1993; Griffiths 1994) and potamodromous species, e.g. roach movements vary from diel movements of less than a kilometre (Baade & Friedrich 1998) to breeding migrations of several hundred kilometres (Mills 1991). Lucas & Baras (2001) note that many species that show limited movements elsewhere exhibit extensive migrations at arctic and subarctic latitudes. The simultaneous migrations of six species, including salmonids, cyprinids and eels, in a river indicate the importance that environmental conditions can have on migratory behaviour (Montgomery *et al.* 1983).

Habitat permanence/seasonality and migratory abilities have been linked in many taxa, e.g. arthropods (Southwood 1962), emydid turtles (Ernst, Lovich & Barbour 1994; cited by Stephens & Wiens 2003) and bird assemblages (Hurlbert & Haskell 2003). Cohen & Johnston (1987) argued that selection for good dispersal ability occurs in most lakes because they are geologically ephemeral, and that good dispersers are less likely to

speciate. Ribera, Foster & Vogler (2003) and Ribera & Vogler (2000) showed for Iberia and for Europe as a whole that species richness in aquatic beetles was greater in riverine than in lake species. They suggested that this was due to the relative impermanence of still water habitats, which selects for species with good dispersal abilities. The scarcity of lacustrine specialist fish, which reflects the impermanence of all but the largest lakes on a geological time scale (Smith 1981; Matthews 1998; Moyle & Cech 2000), is consistent with this pattern.

Mora *et al.* (2003) showed that dispersal from a biodiversity hotspot accounted for much of the observed variation in the species richness of reef fishes while McDowall (2002) showed that the distribution of southern temperate freshwater fish faunas is consistent with an important role for dispersal. On a smaller scale Main (1989) noted a latitudinal decline in species richness of freshwater fish in the South Island of New Zealand, which was attributable to a decline in the number of nondiadromous species. Species-poor West African rivers tend to be inhabited by widespread species (Hugueny 1990).

As the largest rivers in Europe are found at mid-latitudes the distances between spawning and feeding habitats should be greatest in these areas and consequently one would expect most potamodromous species to occur there, as they do (Fig. 7a). Roff (1988) predicted that migratory species should be large, mature late and grow rapidly, a conclusion consistent with the findings of Winemiller & Rose (1992) and this analysis. Bernatchez & Dodson (1987) demonstrated a correlation between body size and migration distance and calculated that large fish had lower migratory costs per unit distance: 42% of the variance in migration distance was accounted for by body mass. Mahon (1984) and Moyle & Herbold (1987) noted that spawning migrations are more common in Europe and western North America than in eastern North America. These differences were associated with lower species richness and larger body size in Europe.

As in Europe, body size increases with latitude in North American freshwater fish (Winemiller & Rose 1992; Taylor & Gotelli 1994). Cardillo (2002) showed a significant latitudinal increase in mean body size of New World birds towards the north due to a relatively greater decline in the numbers of small and medium sized species, a pattern similar to that observed in European fish. Largely with respect to birds Gaston & Blackburn (2000) reviewed five mechanisms that might generate latitudinal variation in body size distributions. They concluded that differential migration abilities are unlikely to account for latitudinal size gradients. The contrast with fish, where there are strong links between latitude, size and migratory ability, probably reflects the much greater vagility of birds: any historical latitudinal differences in species richness and size distributions that might have occurred after glaciation in birds due to differences in dispersal abilities have long since disappeared. Hawkins & Porter (2003) similarly

attributed the greater contribution of glacial history to species richness patterns in North American mammals than birds to the greater vagility of the latter.

Range size–body size relations have been previously reported for North American freshwater fish (McAllister *et al.* 1986; Taylor & Gotelli 1994; Pyron 1999; Rosenfield 2002) and other taxa (Gaston 2003; Gaston & Blackburn 2000; Olifiers, Vieira & Grelle 2004). However, in European fish species the overall and across habitat group relationships occur not because of a direct size effect but because migratory species in each habitat group tend to be larger than residents (Table 5). The effect of migration category has not been considered previously though Hugueny (1990) showed a positive relation between range size and body size in West African freshwater fishes and linked this to the greater dispersal ability of larger fish.

#### PROCESSES

The problem of separating the roles of ecology and history occurs at both species and assemblage levels. Are groups such as salmonids and coregonids more important in northern Europe because they are better at getting there or because they are cold-water specialists? Oberdorff *et al.* (1997) examined the effectiveness of species–area, species–energy and historical hypotheses in explaining species richness in riverine fish and found evidence for all three hypotheses. Larger catchments had more species than small ones and tributaries more species than whole catchments of the same area. This, by itself, could generate a latitudinal trend in species richness, given the smaller, probably more linear, rivers in northern areas. However, growing season temperatures and (terrestrial) productivity show a similar trend, consistent with a species energy explanation, while it is the more northern regions that were glaciated. Sax (2001) has shown that latitudinal gradients similar to those observed in native species occur in a variety of introduced taxa, including North American fishes, arguing against an historical explanation. While the positive correlation between glaciated and unglaciated range areas (Fig. 13) might suggest that ecology plays a major role in determining the current distribution of European fish it should be noted that the trend in Fig. 13 is due almost entirely to generalist species. It is hard to explain the scarcity of riverine species in glaciated areas and their rapid decline with distance from the source area other than by history.

The riverine fish faunas of the glaciated regions of Europe and North America are species poor and have larger, more migratory species that do not exhibit parental care compared with those of the unglaciated Missouri-Mississippi basin (Moyle & Herbold 1987), consistent with the effects of glaciation found in European fish. Mahon (1984) found similar differences in a comparison of rivers in Ontario and Poland: both areas were glaciated but Ontario was less isolated from the Mississippian and Atlantic refugia than Poland from the Danube basin.

McAllister *et al.* (1986) noted that over 120 localized endemics occur in unglaciated regions of North America compared with six in glaciated regions: the two regions are of similar area. The high levels of endemism in the unglaciated barrier regions of Europe has already been mentioned, with 88% of the fauna consisting of endemics: only two endemics are found in the glaciated areas, both in region 4. This pattern is consistent with Rapoport's rule and with the climatic variability hypothesis (Gaston 2003) as the climate of these Mediterranean regions is more seasonal than that of the unglaciated regions to the north. The concentration of endemics in barrier regions and their greater frequency in the mountainous regions 1, 5 and 6, with many small catchments, suggests that isolation could be an important factor.

What are the evolutionary consequences of depauperate fish faunas in previously glaciated areas? One would expect species in these areas to be subject to ecological release and occupy vacant niches, show increased levels of intraspecific variability related to resource polymorphisms and, in the long term, to show increased rates of speciation. Species in these areas show higher levels of polymorphism (Griffiths 1994; Robinson & Wilson 1994; Robinson & Schluter 2000). Robinson & Schluter (2000) noted that 94% of the trophic polymorphisms they recorded occurred in formerly glaciated areas while Griffiths (1994) showed that size polymorphism in Arctic charr *Salvelinus alpinus* was more frequent in species-poor lakes. In North American freshwater fishes glaciation depressed nucleotide diversity and effective population size but the data indicated that speciation events have occurred recently in deglaciated habitats (Bernatchez & Wilson 1998). The low species richness of glaciated regions is generally regarded as a consequence of the limited time since the last glaciation rather than latitudinally linked variation in rates of molecular evolution (Bromham & Cardillo 2003; Stephens & Wiens 2003). The scarcity of endemics in glaciated regions also suggests that insufficient time has elapsed for speciation but one would expect northern species to undergo ecological adaptive radiations in the future provided no further glaciations occur. Five of nine families of North American freshwater fish show evolutionary trends of decreasing body size (Pyron 1999; Knouft & Page 2003), consistent with the hypothesis that colonization of glaciated areas by more vagile large species was followed by adaptive radiation (though Gotelli & Pyron (1991) found the opposite trend in North American minnows *Notropis*). Species with small range sizes are more likely to speciate because of reduced dispersal and lower densities (Gaston 2003).

Glaciation was not a single event but occurred in repeated cycles interspersed with warmer interglacial periods (Dynesius & Jansson 2000). Robinson & Schluter (2000) suggest that these climatic changes and the resulting cycles of range expansion and contraction may have favoured the evolution of a 'glacial genotype' in northern species: such species should be good dispersers

and ecological generalists, capable of exploiting a variety of ecological niches (Dynesius & Jansson 2000). The data presented here are consistent with this hypothesis: northern faunas are dominated by migratory habitat generalists and these have greater range areas than resident or habitat specialist (riverine) species. Such a genotype may be phenotypically plastic (Robinson & Parsons 2002).

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