Body size distributions in North American freshwater fish: large-scale factors

David Griffiths*

School of Environmental Sciences, University of Ulster, Coleraine BT52 1SA, UK

ABSTRACT

Aim To document continental- and regional-scale variation in the size distributions of freshwater fish and examine some energetic, evolutionary and biogeographic explanations for these patterns.

Location North America.

Methods Regional species lists, coupled with habitat and body size information, were used to document the spatial patterns.

Results At the continental scale, riverine specialist fishes show a unimodal, right-skewed, body size distribution whereas habitat generalist and lacustrine specialist species exhibit bimodal size distributions, with only a slight preponderance of small-mode species. Most large-mode species are migratory. Resident species, unlike migratory ones, show a latitudinal increase in mean size, but the size increase across all species is steeper because the importance of large migratory species increases with latitude. Size distributions change from right- to left-skewed with increasing latitude. Maximum body size does not change with increasing family richness but minimum size declines and skewness increases, consistent with diversification of small species. Skewness does not vary with mean family body size.

Main conclusions Post-glacial recolonization by large, habitat generalist, migratory species is the main determinant of latitudinal size distribution trends. There is little support for the energetic hypothesis, but the data are consistent with a negative Cope’s rule.

Keywords Bimodality, freshwater fish, glaciation, habitat preference, kurtosis, migration, North America, recolonization, skew.

INTRODUCTION

Inter-specific increases in the mean body size of species with increasing latitude (Bergmann’s rule, sensu Blackburn et al., 1999) have been found in many, but not all, taxa, including freshwater fish (Lindsey, 1966; Knouft, 2004), although only limited support has been found for Bergmann’s proposed mechanism. As McDowall (1994) and Knouft (2004) have shown for North American freshwater fish (NAFF), changes in mean size are accompanied by changes in the shape of assemblage size distributions. Studies over many taxa have found the majority of distributions to be right-skewed (e.g. Knouft & Page, 2003; Fu et al., 2004; Griffiths, 2006, for freshwater fish examples), although the shape varies with spatial scale, biome, habitat structure, latitude, evolutionary history and trophic and taxonomic levels (Brown & Nicoletto, 1991; Marquet & Cofré, 1999; Bakker & Kelt, 2000; Gaston & Blackburn, 2000; Silva et al., 2001; Knouft, 2004). While early analyses assumed unimodal distributions, it has become clear that many size distributions have more than one mode (Griffiths, 1986; Holling, 1992) and, more recently, analyses have focused on gaps between modes (Allen & Holling, 2008). Skew in multimodal distributions results mainly from differences in the relative contributions of the modal groups rather than changes in the shape of component modes.

A variety of competing, but non-exclusive, hypotheses have been proposed to explain the shape of species size distributions (Allen et al., 2006), which can be classified as energetic, evolutionary, biogeographic, habitat structural and biotic. The energetic hypothesis argues that, for a given taxon and environment,
there is an optimal body size and a right-skewed distribution (Brown et al., 1993), with deviations from the optimum being driven by biotic interactions (Marquet et al., 2008). Some evolutionary hypotheses propose that body size is a relatively conservative trait, variation in regional size distributions reflecting the spatial and/or taxonomic origins of the component species (Marquet & Cofré, 1999; Siemann & Brown, 1999). However, phylogenetic size increases (Cope’s rule) have been noted by many (see Rensch, 1959; Stanley, 1973), with size increases linked to increasing right skew (Stanley, 1973; Kozłowski & Gawełczyk, 2002) and to increasing species richness (McClain & Boryer, 2009). Biogeographic hypotheses, which operate on shorter time-scales, suggest that size distributions are determined by the effects of geography and history on the distribution of different-sized species. Habitat structure can influence the sizes of organisms that an environment can support (e.g. Polo & Carrascal, 1999). Finally, biotic hypotheses propose that size distributions are influenced by competitive, predatory and/or trophic-level interactions. Multimodal distributions, which can be found at all scales, have been suggested to result from, for example, the energetic costs of different modes of locomotion (Lovegrove & Haines, 2004), mixing of faunas across faunal provinces (Marquet & Cofré, 1999), differences in environmental structure and process (Holling, 1992) or size differences associated with trophic level (Griffiths, 1986).

Despite an extensive literature, few have evaluated the determinants of size distributions at a variety of scales for a single group of organisms. In NAFF the latitudinal species richness gradient reflects speciation and extinction events in southern faunas and a post-glacial recolonization gradient in more northern regions (Griffiths, 2010). The recolonizers are predominantly generalist (species found in rivers and lakes), large-habitat (large rivers and lakes), large-bodied and migratory (to and from the sea, diadromous, or along rivers, potamodromous) species, a conclusion also reached for European freshwater fish (Griffiths, 2006). For energetic reasons, vagile species are more likely to be large bodied (Bernatchez & Dodson, 1987; Roff, 1988, 1991). Consequently, the shape of NAFF size distributions should vary with habitat preference. Riverine specialists, which are predominantly resident (Griffiths, 2010), are likely to be unimodally distributed and right skewed, for a variety of reasons mentioned above, while habitat generalists should show a bimodal size distribution, due to an additional mode of large migrant species.

Knouft (2004) demonstrated an increase in mean body size and a shift from right to left skew in NAFF with increasing latitude, trends which were attributed in part to family-level differences in distribution. This paper also examines large-scale spatial trends in the mean size and shape of regional species assemblages but focuses on three biogeographic and evolutionary reasons why a latitudinal trend in mean assemblage body size might occur. Firstly, post-glacial recolonization might be incomplete, with the most northerly regions dominated by large, vagile, species (Griffiths, 2010). Alternatively, post-glacial recolonization might be complete but the increased seasonality associated with northern latitudes favours migration (Jocque et al., 2010) and hence larger species. These hypotheses make similar predictions about trends in body size. However, climatic processes should generate a smooth latitudinal trend whereas the imprint of glaciation is more likely to be detected in size structure and richness if historical effects are still important. Both processes will generate latitudinal trends in size variability and in skewness by affecting the relative abundances of large and small species. Finally, insufficient time has elapsed for extensive post-glacial speciation to occur in northern areas. Speciation in NAFF usually occurs in small channels and at small body sizes (Knouft & Page, 2003; Griffiths, 2010) and could thus generate a latitudinal size trend and skewed distributions. If endemics, which are found predominantly in small channels (Griffiths, 2010), are smaller than average this could also contribute to a size gradient, since they are largely restricted to unglaciated areas (McAllister et al., 1986). Over time, skewed size distributions could result from passive diffusion from a constrained minimum size (Stanley, 1973). Clauset & Erwin (2008) also assumed a lower size limit set by taxon-specific constraints, but suggested that the upper limit is set by an increased risk of extinction at large sizes, counter-balanced by the ecological advantages of large size. These evolutionary hypotheses predict correlations between mean size, skewness and richness at, for example, the family level.

**METHODS**

**Data**

I used the dataset analysed in Griffiths (2010). Mayden (1992) recognized 15 faunal provinces for freshwater fish in North America: some of the provinces described by Hocutt & Wiley (1986) were subdivided to create 48 regions (see Griffiths, 2010, for details). Regional presence–absence lists for 965 native fish species came from Hocutt & Wiley (1986) and Miller et al. (2005). Incomplete species lists, and additions since the Hocutt & Wiley book was compiled, could bias distributional and size estimates (J. Knouft, personal communication). To test this, the North American Native Fish Association checklist (http://www.nanfa.org/checklist.shtml, accessed 14 January 2011) of 1090 extant native freshwater species was treated as complete. Part of the difference in species numbers between the checklist and my dataset reflects uncertainty in determining the status of species which occasionally enter freshwater. I only found information on maximum adult body size, range size, latitude and habitat (see below) for 28 of the species identified since Hocutt & Wiley compiled their lists. These additional 28 species were significantly smaller (mean length 5.7 vs. 14.2 cm), more southern (mean latitude 26.5 vs. 33.4° N), had smaller ranges (295,801 vs. 758,577 km2) and were more likely to be riverine than the species used in my dataset. However, the bias resulting from the omission of these species only tends to reduce the strength of the patterns documented here.

Page & Burr (1991) was the primary source of information on maximum fish (total) length and habitat preference. While there is often considerable intra-specific size variation within a species
range, there is little evidence of any systematic variation in maximum size with latitude (Belk & Houston, 2002) and simulations by Knouft (2004) suggest that intra-specific size variation is unlikely to affect large-scale variation in inter-specific size distributions. Species habitat preferences were identified as riverine, lacustrine or generalist (found in both rivers and lakes).

Regions were identified as glaciated or unglaciated depending on whether or not they were covered by ice at the Last Glacial Maximum (Glaciation). To test for an isolation effect (Connectivity), species richness and composition in highly connected inland regions (those within the Mississippi Basin) and more isolated coastal regions, i.e. regions with rivers discharging directly to the sea, were compared. Because of marked differences in species richness (Briggs, 1986; Griffiths, 2010) regions were also grouped as Pacific, Arctic (Yukon to Labrador) or Atlantic drainage areas, depending on where river systems discharged into the sea (Drainage).

Recolonization results from species movements, which can be undirected and small scale or directed and possibly large scale (Lucas & Baras, 2001). I assumed that colonization rates would be proportional to the most extensive movements species will make in the course of their life, i.e. migratory movements. Nikolsky (1963), Scott & Grossman (1973), Smith (1991), Northcote (1997), McDowall (1988) and Lucas & Baras (2001) were used to identify whether species are diadromous (migrate between sea and freshwater during their life cycle), potamodromous (migrate along river channels) or resident (species which show no more than local movements). Species not identified as diadromous or potamodromous were assumed to be resident.

Analyses

Body size, whether using linear or mass measures, is skewed but can be brought closer to normality by log-transformation, although some deviation tends to remain. In addition, it makes biological sense to use a multiplicative scale (Griffiths, 1986; Kerkhoff & Enquist, 2009). The shape of a distribution can be summarized by its moments [mean, variance (SD2), skewness (g1) and kurtosis (g2)]: for presentational reasons I used the standard deviation (SD) as a measure of the second moment. Positive values of skewness indicate right-skewed distributions. Positive kurtosis (leptokurtic) values indicate distributions which are more peaked than a normal distribution, while negative values (platykurtosis) denote frequencies around the mean that are less than expected for a normal distribution: platykurtic distributions might indicate bimodality in the data. The standard error of g2 is twice that of g1 (Sokal & Rohlf, 1995), making detection of significant kurtosis less likely for a given sample size. A number of statistical procedures have been adopted to test for deviations from unimodality (Hartigan & Hartigan, 1985; Silverman, 1986; Fisher & Marron, 2001). However, because they tend to be conservative, sensitive to non-normality and spatial separation of the modal groups, and to sample size (Jackson et al., 1989; Cheng & Hall, 1998), I report only values of kurtosis and note that platykurtic distributions are not necessarily bimodal.

In bimodal distributions, species with log length ≥ 1.5 (31.6 cm), taken as the trough between the modes, were identified as large-mode species. To test for trends within small-mode fish (log length < 1.5) the numbers of species in 0.2 log size classes (0.4–0.59, etc. up to 1.2–1.39) were calculated.

To test whether latitudinal trends in maximum and minimum body size were simply due to changes in species richness, 100 samples for each region, of size equal to the regional resident or migratory pools, were taken at random from the observed continental species pools and the mean maximum and mean minimum sizes calculated. These mean values were regressed against regional latitude and compared with the observed maximum and minimum values by analysis of covariance. A similar analysis was performed to test whether maximum and minimum size changed with family richness.

All lengths are in cm, logarithmic transformations are to the base 10, all interval estimates are standard errors unless otherwise indicated and all nonlinear trend lines in the figures are fitted by locally weighted scatterplot smoothing (LOWESS). Most size distributions are non-normal, but the conclusions reached using nonparametric tests did not differ from those obtained by the more powerful parametric tests. All statistical tests of percentage data were carried out on arcsine-square root transformed values. The analyses make no allowance for spatial dependence in the data, thus probably weakening the strength of the relationships detected (Hawkins et al., 2007). Contour maps were drawn using SURFER version 7.0 (Golden Software Inc.), with interpolation by kriging and plotting using the medium smoothing option: for technical reasons the Arctic Archipelago and other islands were excluded when drawing contours.

RESULTS

Continental-scale patterns

The overall size distribution for NAFF is markedly right skewed (see Fig. 1 in Knouft & Page, 2003). This skew is largely due to riverine species, whereas the less numerous habitat generalists show a distinct bimodality in size (Fig. 1). There is a size mode at about 10 cm for both habitat preference types and an upper mode at around 50 cm in generalists. Lacustrine specialists also tend to be bimodal in size. Bimodality appears to be more marked in riverine species in Pacific than in Atlantic drainages (see Fig. S1 in Supporting Information).

When species are classified by migration category there is no evidence of bimodality (Fig. 2). Residents are significantly smaller than diadromous and potamodromous species (F_{2,86} = 187.10, P < 0.001). Migrant mean size varies nonlinearly with latitude (see below): after adjusting for this potamodromous species are found to be larger than diadromous species (difference in regional mean log lengths between migration categories = 0.12, t = 3.51, n = 47, P = 0.001). The size distributions for riverine and resident species are of similar shape (Fig. 2a), because riverine species tend to be resident. Similarly, migratory species are predominantly habitat generalists (Fig. 2b,c): the bimodality results from a mixture of small resident and large...
migratory species (Fig. 1, Table 1). This is not the case for lacustrine species. Despite migrants increasing the skewness and kurtosis of riverine species, resident riverine body size remains right-skewed and leptokurtic. Furthermore, migratory generalists are significantly left-skewed (Table 1).

Table 1  Moments of (log) body size distributions for fish classified by habitat preference and migratory category.

<table>
<thead>
<tr>
<th></th>
<th>Riverine</th>
<th>Generalist</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Resident</td>
<td>Migratory</td>
</tr>
<tr>
<td>Mean</td>
<td>1.02</td>
<td>1.70</td>
</tr>
<tr>
<td>SD</td>
<td>0.32</td>
<td>0.45</td>
</tr>
<tr>
<td>Skewness</td>
<td>$1.06 \pm 0.11^*$</td>
<td>$0.28 \pm 0.39$</td>
</tr>
<tr>
<td>Kurtosis</td>
<td>$1.31 \pm 0.22^*$</td>
<td>$-0.11 \pm 0.77$</td>
</tr>
<tr>
<td>$n$</td>
<td>507</td>
<td>36</td>
</tr>
</tbody>
</table>

*$P < 0.05$.

Maximum size is independent of family species richness, but mean and minimum lengths decline, and the size range increases with richness (maximum $r = 0.06, P > 0.5$; mean $-0.38, P < 0.01$; minimum $-0.62, P < 0.001$; range $0.91, P < 0.001$, $n = 48$): the same trends were found for genera.
data generated significant trends in maximum and minimum size with family richness ($r = 0.99, -0.96$, $n = 48, P < 0.001$, respectively), indicating that the absence of a trend in observed maximum size is not a sampling artefact. The minimum size and slope of the size–family richness trend were significantly greater than those of randomized data because species-poor families had larger species than expected (slope $F_{1,22} = 5.55, P < 0.05$, intercept $F_{1,22} = 44.68, P < 0.001$). Based on families with eight or more species, skewness increases with species richness ($r = 0.51, n = 18, P < 0.05$). The minimum size for these families varies from 2 to 86 cm; however, skewness does not vary with mean family body size ($r = -0.30, n = 18, P > 0.2$), inconsistent with passive diffusion from a minimum, class level, size constraint. Furthermore, the relative size range is independent of body size, with the mean maximum length being 8.2 times the minimum (95% limits 5.7–11.7 times).

Regional-scale patterns

The overall regional size distributions show clear latitudinal trends in shape (see Fig. S2): means increase but SD and skewness decline. Although the moments for riverine and generalist species show marked changes at the continental scale (Fig. 3), only the means are correlated (mean $r = 0.49, P = 0.001$; SD $r = 0.12, P > 0.2$; skewness $r = 0.08, P > 0.2$; kurtosis $r = 0.09, P > 0.2$, $n = 42$). All riverine species are right skewed, whereas generalists show left skew above mid-latitudes. Platykurtosis (and bimodality; see Fig. S3) is found predominantly in interior drainages in riverine species, but is the norm for generalists (Fig. 3). There is a significant negative correlation between the percentage of potamodromous species in riverine assemblages and the degree of platykurtosis ($r = -0.57, n = 42, P < 0.001$), again indicating that bimodality results from the inclusion of migrants.

The mean size of residents and migratory species is greater in inland than coastal regions ($F_{1,43} = 49.91, P < 0.001, F_{1,43} = 12.36$, $P = 0.001$, respectively; latitude as a covariate). In coastal regions the mean size of residents increases to the north but there is no trend for migrants ($r = 0.68, n = 24, P < 0.001; r = 0.14, n = 24, P > 0.5$, respectively; Fig. 4a). The increase in resident size with latitude (Fig. 4a) is largely a consequence of differences in the mean size of species which occur only in unglaciated regions, or are widespread, or occur only in glaciated regions (means 1.00 $\pm$ 0.01, $n = 644$; 1.21 $\pm$ 0.03, $n = 187$; 1.52 $\pm$ 0.05, $n = 15$, respectively) since there is a significant latitudinal trend only for species restricted to unglaciated areas ($r = 0.10, P < 0.05; r = 0.02, P > 0.5$; $r = 0.02, P > 0.5$, respectively). However, mean length across all species changes more rapidly than for either migration category because of the increasing importance of migrants at high latitudes. Mean regional size increases with the percentages of migratory and generalist species, and varies with glaciation, connectivity and drainage (Table 2): on average species are larger in inland regions (Mississippi Basin) and those draining to the Pacific. While there is a significant correlation between the regional percentages of migratory and generalist species ($r = 0.65, n = 48, P < 0.001$), inclusion of both variables in the model explains significantly more of the variation in regional body size ($\Delta AIC_{c} = 18.0$). Habitat generalists increasingly dominate faunas towards the pole ($r = 0.71, n = 48, P < 0.001$), their contribution rising from 20% in the southernmost regions to 80% in the Arctic. Similarly the percentage of migratory species increases from 10 to 90% ($r = 0.90, n = 48, P < 0.001$). Overall, generalists are much bigger than riverine specialists in unglaciated regions:

![Figure 3](image-url) Continental-scale variation in the mean, skewness and kurtosis of size distributions for riverine (top) and generalist species (bottom). Shaded areas show negative values of the moments (i.e. left skew or platykurtosis).

Table 2 General linear model of the effects of migration category, habitat preference, glaciation, catchment and drainage on mean (log) regional body size in North American freshwater fish ($R^2 = 0.98$). Least-squares means, adjusted to the means of the covariates, are shown in the bottom table.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Migratory species</td>
<td>1</td>
<td>0.145</td>
<td>194.88</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>% Generalist species</td>
<td>1</td>
<td>0.015</td>
<td>20.73</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Glaciation</td>
<td>1</td>
<td>0.012</td>
<td>15.91</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Connectivity</td>
<td>1</td>
<td>0.020</td>
<td>27.42</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Drainage</td>
<td>2</td>
<td>0.011</td>
<td>15.34</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Glaciation × % generalist species</td>
<td>1</td>
<td>0.015</td>
<td>19.69</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Error</td>
<td>40</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Least squares means ± SE  $n$

<table>
<thead>
<tr>
<th>Connectivity</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal</td>
<td>1.42 ± 0.01</td>
<td>23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inland</td>
<td>1.48 ± 0.01</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drainage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atlantic</td>
<td>1.41 ± 0.01</td>
<td>34</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic</td>
<td>1.45 ± 0.02</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific</td>
<td>1.50 ± 0.02</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

However, this difference disappears in glaciated faunas (Fig. 5, interaction term in Table 2) due to the loss of small species. There are significant, convergent, latitudinal trends in minimum and maximum body sizes for resident species (slopes $0.017 ± 0.001$, $-0.022 ± 0.003$, $F_{1,92} = 109.71, P < 0.001$), but no trends or convergence for migratory species (Fig. 4b; slopes $-0.005 ± 0.003$, $-0.003 ± 0.002$, $F_{1,92} = 0.15, P > 0.5$). Similar scaling relations were found in random samples from continental species pools, but the observed maximum and minimum sizes were greater than those of random samples from the resident species pool, while the observed minimum was less than from the migratory species pool (see Table S1): the maximum size of migrants was as expected for a random sample. These conclusions do not change when the rather different Mexican and Sonoran regional faunas are omitted from the species pools. While the size limits for migratory species do not change with latitude, the moments do (parabolic relationships for all moments except skewness, which declines monotonically), suggesting that the distributions are not random samples from a fixed pool of migratory species. All of the distributions for the 24 regions comprising the Mississippi Basin are platykurtic (13 significantly so; mean kurtosis ± 95% CI, $-1.01 ± 0.13, n = 24$) and bimodal (see Fig. S4). This bimodality is due to migratory species being much larger than residents, rather than to bimodality (as indicated by negative kurtosis) within each category: mean kurtosis (± 95% CI), for migratory (0.93 ± 0.37) and resident (0.01 ± 0.19) species. The degree of skewness in Mississippi regional faunas is strongly correlated with species richness ($r = 0.91, n = 24, P < 0.001$), the more impoverished northern and western regions having proportionally more large migratory species (richness–% migratory species $r = -0.74, n = 24, P < 0.001$). Endemics (species restricted to one region) are significantly smaller than non-endemic species (regions ≥ 35° N means 15.2, 21.4 cm, $F_{1,47} = 15.64, P < 0.001$; regions < 35° N means 8.6, 14.4 cm, $F_{1,40} = 31.88, P < 0.001$; latitude as a covariate) and endemics affect the latitudinal trends in mean size and skewness (see Fig. S5).

Body size trends depend both on the relative contributions of the modal groups and, to a lesser extent, on distributional trends within modes. Large-mode species richness exceeds that of small-mode species richness above about 45° N (Fig. 6). Below 35° N, there is no trend in regional richness of small-mode species, whereas that of large-mode species declines (slopes $0.005 ± 0.011$, $0.024 ± 0.009, n = 13, P > 0.5, < 0.05$, respectively). These changes in the relative importance of the two size groups largely generate the latitudinal trend in skewness ($r = -0.90, n = 48, P < 0.001$). There are also trends within modes: even for small-mode species below 35° N, the percentage of species in the smaller size classes increases more rapidly to the south (slopes; latitude $-0.395 ± 0.203, t = 1.95, P = 0.06$; size × latitude $0.067 ± 0.023, t = 2.96, P < 0.01$).

**DISCUSSION**

This paper focuses on some of the large-scale processes considered by Allen et al. (2006). Griffiths (2010) concluded that species richness patterns of NAFF were organized at different scales between the relatively young, glaciated and the older, less disturbed, unglaciated environments, with biogeographic processes being more important in the former and evolutionary ones in the latter areas.

Knouft (2004) demonstrated that the mean size of NAFF species assemblages increased and skewness changed from right to left skew with increasing latitude. The current analyses, though based on regional rather than grid square species lists, extend these conclusions by showing that these trends vary with the degree of habitat specialization, migratory tendency and endemism across species and whether or not regions were glaciated. The bimodality in generalist (Fig. 1b) and some riverine species assemblages (see Fig. S3) is due to (larger) migratory species. However, the bimodality in lacustrine species is not attributable to migratory species (Fig. 1c), but probably to trophic processes. The significant variation in body size with connectivity and drainage (Table 2) is expected because of the strong association between migration and size (Griffiths, 2010) and because the percentage of migrants is greatest in the Pacific. As expected from their habitat preference (Griffiths, 2010), endemics are smaller than more widespread species. Resident species are expected to slowly recolonize glaciated areas by a variety of means, as outlined in Griffiths (2010), but whether this will generate a latitudinal size gradient is unclear. The inland regions of the Mississippi Basin acted as a centre of post-glacial colonization for many other regions of North America (Robison, 1986) and their greater mean size and bimodal size distributions are a consequence of the greater proportion of large, potamodromous, species there.
The energetic hypothesis (Brown et al., 1993; Kelt & Brown, 1998) argues that species evolve to an optimal size because of taxon-level energetic acquisition and allocation constraints. This model, which has been heavily criticized by some on theoretical and empirical grounds (Kozłowski, 2002, and references therein), generates right-skewed distributions, although the shape is influenced by a range of biotic factors (Allen et al., 2006). For example, Marquet et al. (2008) showed that, with increasing energy limitation, the energetic model predicts a decline in the, albeit still positive, skew. The latitudinal convergence in maximum and minimum body size for resident species (Fig. 4b) could be taken as evidence of an ‘optimal’ body size (of 22 cm, or 113 g, assuming $W = 0.00001 L^3$) but this ‘optimal’ size is considerably above the modal size observed for residents (Fig. 2) and is rather closer to the trough between modes, even in Arctic regions. Furthermore, these trends can also be generated by a sample size effect. Observed size minima for residents are greater and the latitudinal slope steeper than expected by chance, suggesting a disadvantage and/or dispersal limitation of small-sized species, particularly in northern regions. Large fish are energetically more efficient migrants than small species (Bernatchez & Dodson, 1987; Roff, 1988, 1991) and, as expected, migrants dominate the large size mode. The latitudinal changes in skewness and kurtosis result from changes in the proportions of small resident and large migratory species, with a small effect of endemism in unglaciated areas.

Body size can change appreciably over evolutionary time. Cope’s rule, the evolutionary tendency for body size to increase, while contentious, has been claimed in many taxa (Rensch, 1959; Stanley, 1973). However, Jablonski (1997) found that a majority of Cretaceous marine mollusc lineages showed no trend in mean size, although variance increased, and that decreases in mean size were as common as increases. Knouft & Page (2003), examining nine families with 85% of NAFF species, found a decrease in size in five and no change in the remaining four families, two of which were initially small. Stanley (1973) stated that taxa composed of large species tend to be specialized, but short-lived in evolutionary terms: this is the converse of the pattern in NAFF (Griffiths, 2010). More recently, various authors (Knouft & Page, 2003; Knouft, 2004; references in Griffiths, 2010) have argued that there have been radiations from fish species characteristic of large, relatively long-lived, habitats (large river channels) to those found in smaller, more isolated and shorter-lived streams, favouring smaller-bodied species, i.e. an inverse Cope’s
rule. The decrease in minimum body size with increasing family richness and the absence of a trend in maximum size shown here are consistent with this hypothesis. Since NAFF richness is greatest in undisturbed long-lived habitats, e.g. rivers in unglaciated areas south of 35° N, and small species are more likely to persist in relatively undisturbed regions, e.g. unglaciated ones (Griffiths, 2010), size trends should be most apparent there. In support, the minimum size of resident fishes decreases to the south (Fig. 4b), consistent with a greater diversification of small fish, although also with the converse, a loss of small species as the distance to the ice sheets declines.

Stanley (1973) noted that evolutionary size increase was associated with increasing positive skew. Right-skewed size distributions can result in part from the ecological advantages of large size counter-balanced by an increased risk of extinction at large sizes (Claustr & Erwin, 2008), but Kozlowski & Gavelczyk (2002) showed that such distributions can also be produced when small species are more extinction prone. Although contemporaneous selection pressures favouring larger sizes (Kingsolver & Pfennig, 2004) and increased extinction rates in larger sized taxa (Cardillo et al., 2005; Liow et al., 2008) are consistent with the Clauset & Erwin model, diversification to larger sizes, i.e. Cope’s rule, is not the dominant process in NAFF. While the existence of a lower size limit is possible across major taxa, e.g. vertebrate classes, cladogenetic diffusion from that limit seems insufficient to explain the 40-fold variation in minimum length and independence of body size range on body size reported here. If there is a constraint on small size, small-bodied taxa should be right skewed, but larger-bodied taxa, because they are further from the constraint, should be less skewed, i.e. there should be a positive correlation across taxa between skewness and body size (Kozlowski & Gavelczyk, 2002). There was no such correlation for NAFF families. NAFF show a decline in minimum size and an increase in size range (and skew) with increasing family richness but no trend in maximum size: this is in sharp contrast to the positive trend in maximum size in randomized data. In metazoan phyla and bird and mammal families, minimum size decreases and size range increases with increasing species richness (McCain & Boyer, 2009): maximum sizes increase in Metazoa and birds, but show no trend in mammals.

This paper provides strong evidence that the trends in body size distributions in glaciated areas reflect an increased importance of (large) migrant species in these areas and result from differential dispersal ability. It is likely that glaciation exerted its effects beyond the southern edge of the ice sheets (about 39° N), although it is not clear how far these effects extended. While size increases could also result from seasonality favouring migrants, trends in body size and richness change slope at about 35° N (Figs 5, 6 and S5), more consistent with a glaciation effect, although this remains to be tested.

ACKNOWLEDGEMENTS

My thanks to Simon Blanchet, Christine Griffiths, Jason Knouft and two anonymous referees for helpful comments which greatly improved the manuscript and to Christine Griffiths for setting up Hartigans dip test in R.

REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Body size distributions for riverine and generalist species found in Atlantic and Pacific drainages.

**Figure S2** The moments of regional size distributions show clear latitudinal trends.

**Figure S3** Riverine species assemblages with apparently bimodal regional body size distributions.

**Figure S4** Regional size–frequency distributions within the Mississippi catchment: migratory species are shown in grey.

**Figure S5** Regional variation in the mean length and skewness of all species and non-endemic species as a function of latitude.

**Table S1** Analysis of covariance $F$ statistics from comparison of observed and simulated maximum and minimum size – latitude trends for resident and migratory species.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

**BIOSKETCH**

The author is emeritus reader in freshwater ecology and occasionally writes. He has interests ranging from the small-scale ecology of individual species to biogeography and macroecology, particularly of body size.

Editor: Janne Soininen