

CORRESPONDENCE

Diadromy and genetic diversity in Nearctic and Palearctic fishes: a reply

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In his comments on our study reviewing phylogeographic structure of Nearctic and Palearctic fishes (Bernatchez & Wilson 1998), McDowall (1999) highlights the contribution of diadromous species to our data set. Using linear regression, McDowall reanalysed data from fig. 3 in our study and found no significant relationship between median distributional latitude of diadromous species and nucleotide diversity (McDowall 1999; fig. 1), which apparently contradicts an important conclusion of our study. He goes on to discuss genetic variation of diadromous fish as well as their contribution to boreal fish assemblages, and closes with the suggestion that future phylogeographic studies should explicitly include ecological hypotheses.

We acknowledge the contribution of diadromous species to our data set – as stated in the description of the methodology (Bernatchez & Wilson 1998; p. 438); anadromous species were included despite their potential for marine dispersal, because of their dependence on a freshwater spawning habitat. The fact that the majority of our species can be classified as ‘diadromous’, however, cannot be used to ‘support the hypothesis that the high degree of diadromy at high latitudes results from relatively easier dispersal by diadromous fishes’ (McDowall 1999). Rather, our summary reflects the published data that were available and fit our criteria, i.e. studies of intraspecific mtDNA diversity that encompassed ranges of several hundred square kilometres or more. Although our sampling did not target species a priori, and despite our attempt at broad taxonomic coverage, the data set nonetheless carries inherent taxonomic bias from researcher interest and funding realities (e.g. 16 out of 42 species listed in our Appendix 1 are salmonids). Thus, our data set cannot be used to support, let alone examine, hypotheses regarding the community contribution of diadromous species to boreal fish assemblages.

Despite these limitations, we agree with McDowall’s statement that comparisons between diadromous and nondiadromous species should be informative. Although we appreciate the fact that differences in life history may affect patterns of genetic diversity, we chose not to separate diadromous and freshwater species in our analyses for several reasons. Subdivision of the limited data available would have reduced resolution power, and could potentially have prevented us from being able to draw conclusions relative to the major issues we were interested in; that is, quantifying general trends on the effects of Pleistocene glaciations on genetic diversity. Furthermore, definitions of diadromy are still partly speculative, as demonstrated by McDowall’s discussion of *Morone americana*, and his exclusion of *Coregonus artedii* from his diadromous species set, despite the main source of data for the latter species resulting from a study on anadromous James Bay–Hudson Bay populations (Bernatchez & Dodson 1990). In addition, several species in our data set encompass both truly anadromous and strictly freshwater populations, and the published data available could have come from freshwater populations only (e.g. *Salvelinus fontinalis*), anadromous populations only (e.g. *Salmo salar*), or a combination of both types (e.g. *Coregonus lavaretus*, *Coregonus clupeaformis*, *Osmerus mordax*, *Salmo trutta*, *Salvelinus alpinus*). Under these circumstances, we could not justify subdividing our data set by life-history types.

We support McDowall’s effort to discriminate between patterns of latitudinal diversity gradients for diadromous vs. strictly freshwater fishes, and for the sake of argument have reanalysed our data set, discriminating between diadromous and freshwater fishes as defined by McDowall but including *C. artedii* in the first category. As pointed out by McDowall, there is no significant relationship between mean distributional latitude and nucleotide diversity based on a linear regression for all diadromous species in our data set. An examination of McDowall’s fig. 1 (redrawn from fig. 3 of Bernatchez & Wilson 1998)

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shows that this is largely caused by the low nucleotide diversity values observed among the few diadromous species found at low latitudes ($< 46^\circ$). Nonlinear piecewise regression of McDowall's diadromous subset, however, explained 67% of the variance in nucleotide diversity, refuting his argument of there being no latitudinal effect. Similarly, a significant effect of latitude on nucleotide diversity was observed when only diadromous species above 46° were considered ($y = -0.004x + 0.02995$, $r = -0.4617$, $P = 0.05$). We had also pointed out that, as a group, sturgeon species showed very reduced nucleotide diversity compared to teleost fishes, independent of life history or latitude. Consequently, excluding sturgeon species from this analysis further increased the significance of this relationship ($y = -0.005x + 0.03472$, $r = -0.5346$, $P = 0.02$).

Nevertheless, we also agree with McDowall's view that several aspects of a diadromous life cycle may have contributed to reduce effects of glaciation events compared to strictly freshwater species. As well as facilitating the recolonization of deglaciated regions, the ability of these species to migrate between marine and freshwater environments enables much higher levels of gene flow than naturally occur for strictly freshwater species. Based on nuclear markers, Ward *et al.* (1994) estimated that gene flow within marine fishes was one to two orders of magnitude greater than within freshwater species, and also concluded that glaciation events had much greater impacts on freshwater vs. marine fishes. As well as showing greater intraspecific differentiation and higher G_{ST} values due to fragmentation and restricted gene flow (Ward *et al.* 1994), freshwater fishes also possess greater intraspecific divergence of mitochondrial haplotypes than marine or anadromous species (Billington & Hebert 1991). Low intraspecific mtDNA divergence values within marine species (Ovenden 1990) may be accounted for by coalescence facilitated by high levels of gene flow. Similar processes would also account for low intraspecific divergence within diadromous species, whereas restrictive dispersal conditions for freshwater species would maintain divergent haplotypes in isolated populations. Indeed, detailed examination of data from our Appendix 1 shows that, although nucleon diversity of diadromous and nondiadromous species included in our data set is comparable, the mean intraspecific divergence of strictly freshwater species is almost three-times greater than that for diadromous fishes (Bernatchez & Wilson 1998; p. 451). Despite

the lessened effects of glaciation events on diadromous species, however, it is worth noting that latitudinal gradients are also apparent for evolutionary effective female population size (N_{ef}) and divergence between sister species for both diadromous and nondiadromous species (Bernatchez and Wilson 1998, figs 4 and 5), suggesting that glaciation events had long-term genetic and evolutionary effects on diadromous as well as nondiadromous species.

In conclusion, it is clear that, globally, the patterns of reduced intraspecific nucleotide diversity with latitudinal distribution holds for strictly freshwater, obligatory and facultative anadromous fishes. In saying this, we fully agree with McDowall that differences in life history may also be partly responsible for the observed variance in genetic diversity among species. As we stated previously, 'studies which examine the inter-relationships between ecological and genetic parameters should also prove fruitful' (Bernatchez & Wilson 1998; p. 445). We join with Dr McDowall in encouraging the incorporation of historical, ecological, and phylogenetic hypotheses into future phylogeographic studies, and look forward to the elucidation of the effects of ecological parameters such as life history, body size, generation time, trophic level, and habitat requirements on phylogeographic pattern. Although the data available to date are insufficient to address such issues in detail, future phylogeographic studies framed within these contexts could potentially result in substantial advances for conservation biology and evolutionary ecology.

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