AR-324

Ecology of Freshwater Fish 2010: 19: 390–400
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ECOLOGY OF
FRESHWATER FISH

Life history trait diversity of native freshwater fishes in North America

Mims MC, Olden JD, Shattuck ZR, Poff NL. Life history trait diversity of native freshwater fishes in North America.
Ecology of Freshwater Fish 2010: 19: 390–400. 2010 John Wiley & Sons A/S

Abstract – Freshwater fish diversity is shaped by phylogenetic constraints acting on related taxa and biogeographic constraints operating on regional species pools. In the present study, we use a trait-based approach to examine taxonomic and biogeographic patterns of life history diversity of freshwater fishes in North America (exclusive of Mexico). Multivariate analysis revealed strong support for a tri-lateral continuum model with three end-point strategies defining the equilibrium (low fecundity, high juvenile survivorship), opportunistic (early maturation, low juvenile survivorship), and periodic (late maturation, high fecundity, low juvenile survivorship) life histories. Trait composition and diversity varied greatly between and within major families. Finally, we used occurrence data for large watersheds (*n* = 350) throughout the United States and Canada to examine geographic patterns of life history variation. Distinct patterns of life history strategies were discernible and deemed congruent with biogeographic processes and selection pressures acting on life history strategies of freshwater fishes throughout North America.

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Key words: life history strategies; traits; functional diversity; freshwater fishes; North America

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Accepted for publication March 15, 2010

Introduction

Freshwater fishes are among the most diverse groups of vertebrates in the world, exhibiting extraordinary taxonomic breadth, endemism, and geographic scope in their distribution (Lévêque et al. 2008). Rivalling the taxonomic diversity of freshwater fishes is the wide range of morphological, behavioural, and life history attributes that characterise the constituent species. The rich taxonomic and functional diversity of freshwater fishes stem largely from the fact that streams, rivers, lakes, and wetlands are embedded in terrestrial landscapes which limit the dispersal of freshwater organisms by promoting habitat isolation (Darlington 1948; Berra 2007). This has resulted in biogeographic islands of habitat (water) in which the function and form of freshwater fish species represent the product of differential selection pressures in response to a diverse array of environmental drivers operating across multiple temporal and spatial scales (Hugueny et al. 2010).

There is a long history of scientific inquiry into patterns of trait diversity in freshwater fishes. Some notable efforts include those of Breder & Rosen (1966), who were the first to provide a comprehensive catalogue summarising the reproductive characteristics of most fishes. Balon's (1975) description of the evolution of fish reproductive guilds remains the prime classification of fish reproductive strategies. Guilds were further explored by Wootton (1984), who compiled data on size at maturity, fecundity, egg size, and a number of other reproductive traits for Canadian freshwater fishes. These efforts were followed by Winemiller (1989, 1992) who used life history theory to develop a holistic perspective of linkages between fish traits and environmental gradients. Most recently, Welcomme et al. (2006) defined environmental guilds of freshwater fishes (using reproductive, behavioural, and ecological traits) as a tool for riverine ecological assessment, and Frimpong & Angermeier (2009) presented a database of ecological and life history traits of freshwater fishes of the United States.

The ecology of freshwater fishes has predominantly been studied according to taxonomy (Jackson et al. 2001), but over the past two decades ecologists have increasingly supported the idea that traits, not species

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doi: 10.1111/j.1600-0633.2010.00422.x

entities, may be a more insightful currency of investigation (Olden et al. 2010). Trait-based approaches in basic and applied research offer a framework for mechanistically linking species traits to major environmental drivers that influence organism fitness or performance (McGill et al. 2006). This is supported by the habitat template (templet) model of Southwood (1977, 1988) and life history theory (Pianka 1970; Stearns 1992) that predicts that environments favour specific suites of traits, resulting in the evolution of life history strategies or tactics that enable a species to cope with a range of ecological problems. Winemiller & Rose (1992) identified three primary life history strategies in freshwater fishes that represent the essential trade-offs among the basic demographic parameters of survival, fecundity, and onset and duration of reproduction (Fig. 1). Opportunistic strategists are small-bodied species with early maturation and low juvenile survivorship and are associated with habitats with frequent and intense disturbance. Equilibrium strategists are typically small to medium in body size with moderate age at maturation (relative to other freshwater fish species), low fecundity per spawning event, and high juvenile survivorship largely associated with high parental care and small clutch size. They are predicted to be favoured in more stable habitats with low environmental variation. Periodic strategists are characterised by larger body size, late maturation, high fecundity, and low juvenile survivorship and are often associated with highly periodic (seasonal) environments. The three life history strategies of the continuum can be interpreted as being adaptive with respect to relative variability and predictability of environmental regimes (Winemiller 2005; Fig. 1).

The traits-based perspective presents a powerful paradigm for fish ecology and has gained momentum in its application in recent years. When investigating fish community-environment relationships at large spatial scales, a trait analysis facilitates the comparison of species compositions that naturally differ due to biogeographic constraints on regional species pools (e.g., Vila-Gispert et al. 2002; Tedesco & Hugueny 2006; Tedesco et al. 2008; Ibañez et al. 2009). This allows for comparisons of species from disparate geographies where strategies and adaptations are hypothesised to converge across diverse taxonomies (Lamouroux et al. 2002; Irz et al. 2007; Olden & Kennard 2010). Understanding life history strategies of organisms also goes beyond ecological theory to practical application. Under a particular set of environmental selective forces, specific combinations of traits (strategies) will be favoured in a given population. For example, the trait compositions of fish assemblages have been linked to hydrologic variability (e.g., Poff & Allan 1995), habitat alteration (e.g., Goldstein & Meador 2005) and climate change (e.g., Daufresne et al. 2003), and species traits have been predictive of fish extinctions and invasions (e.g., Angermeier 1995; García-Berthou 2007; Olden et al. 2008). The relationships between environmental selective forces and trait compositions of freshwater fish assemblages provide a basis to develop predictive models to help conserve native species and create risk-assessment protocols for non-native fishes based on generalised population dynamics and responses to environmental conditions (King & McFarlane 2003; Winemiller 2005; Welcomme et al. 2006). Trait-based approaches may also provide the power to elucidate the effects of multiple environmental stressors, as has been shown for invertebrates in lotic ecosystems (Statzner & Bêche 2010).

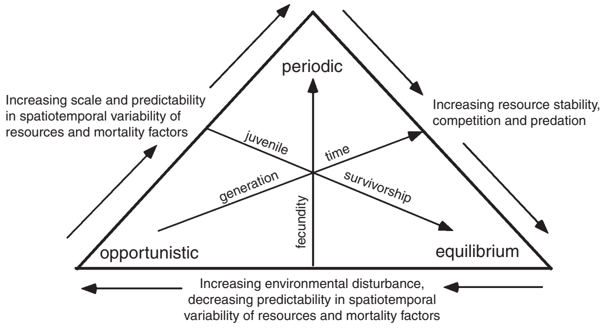


Fig. 1. Life history continuum model adapted from Winemiller (2005) and originally conceptualised in Winemiller & Rose (1992). Inside arrows summarise fundamental trade-offs between juvenile survivorship, generation time, and fecundity that define the three end-point strategies. Outside arrows summarise how selection pressures may favour certain strategies in relation to biotic and abiotic factors.

A necessary precursor to the advancement of trait-based studies in fish ecology is to develop and explore large databases containing ecological and biological traits of species representing a diverse taxonomy. We address this challenge in the present study by examining the taxonomic and geographic patterns of life history trait variation in virtually all freshwater fish species of North America exclusive of Mexico. First, we report on the development of a trait database for 1054 native and non-native fish species of North America according to attributes describing species morphology, reproductive ecology, life history, trophic ecology, and habitat preferences. Next, using a subset of these traits we explore patterns in life history variation among major families of native freshwater fishes. We then assess the life history model of Winemiller & Rose (1992) by asking whether North American fishes conform to the opportunistic-periodic-equilibrium trichotomy of life history strategies. Finally, we examine and compare geographic variability in the distribution of life history strategies according to 350 watersheds in the United States and Canada.

Materials and methods

Database of fish life history traits

We developed a trait database for 1054 native and non-native species of freshwater fishes found in the United States and Canada (according to Nelson et al. 2004; references available upon request from JDO). We defined a freshwater fish broadly to include those species that can reproduce in freshwater and diadromous species that spend the majority of their lives in freshwaters. We excluded numerous species with strong marine or estuarine affinities that may enter freshwaters for only short periods of time. Data were collected for 15 biological (comprising morphological, physiological, and life history traits) and ecological (comprising environmental preferences and associated behaviours) traits that could be justified on the basis of our current knowledge and information available for the majority of species pools. Trait values were represented by ordinal, nominal, or continuous data. Ordinal and nominal traits were assigned a single state based on a majority of evidence rule according to adult preferences, and median values for continuous traits were used when ranges were presented. Trait values for age and length at maturation were recorded for female specimens when possible. Trait assignments were based on a multi-tiered data collection procedure, where a variety of sources were queried in the following order: (i) species accounts in state, provincial, and regional fish accounts (i.e., 'The fishes of…'); (ii) species descriptions from the primary literature, state agency reports, university reports, and graduate theses; (iii) data from reputable electronic databases; and (iv) targeted search of the World Wide Web using the Google Scholar^{TM} search engine. Web searches were conducted for each species using their scientific name as a search query, and all results up through the 80th entry were examined. For species that produced considerably fewer results (<10 records), a new search was conducted using the appropriate common name or other possible 'older' nomenclature. In total, over 300 texts, articles, reports, theses and web sources were used to obtain trait values.

In the present study we focused on the trait diversity of the native species of freshwater fishes (777 species, 32 families, 138 genera, Table 1) according to seven life history attributes describing the co-evolution of traits associated with reproduction. The life history traits included maximum length, length at maturation, longevity, age at maturation, total fecundity, egg size (mean diameter of mature, fully yolked ovarian oocytes), and parental care following Winemiller (1989) (Table 2). Parental care was quantified as the Σx_i for i = 1–3, where $x_1 = 0$ if no special placement of zygotes, $x_1 = 1$ if special placement of zygotes, $x_1 = 2$ if both zygotes and larvae maintained in nest, $x_2 = 0$ if no parental protection of zygotes or larvae, $x_2 = 1$ if brief period of protection by one sex (<1 month), $x_2 = 2$ if long period of protection by one sex (>1 month) or brief care by both sexes, $x_2 = 4$ or lengthy protection by both sexes (>1 month), $x_3 = 0$ if no nutritional contribution to larvae, $x_3 = 2$ if brief period of nutritional contribution to larvae (<1 month), $x_3 = 4$ if long period of nutritional contribution to larvae (1–2 months), and $x_3 = 8$ if extremely long period of nutritional contribution to larvae (>2 months).

Table 1. Families of freshwater fishes included in this study.

Family	Code	Species count	>3 trait (count)	>3 trait (% orig.)
Acipenseridae		7	7	100
Amblyopsidae		6	6	100
Amiidae		1	1	100
Anguillidae		1	1	100
Aphredoderidae		1	1	100
Catostomidae	**CATO**	**62**	**53**	**85**
Centrarchidae	**CENT**	**31**	**29**	**94**
Characidae		1	1	100
Clupeidae		8	8	100
Cottidae	**COTT**	**27**	**19**	**70**
Cyprinidae	**CYPR**	**250**	**176**	**70**
Cyprinodontidae	**CYPT**	**15**	**13**	**87**
Elassomatidae		6	5	83
Esocidae		4	4	100
Fundulidae	**FUND**	**32**	**26**	**81**
Gadidae		2	2	100
Gasterosteidae		4	4	100
Goodeidae		3	2	67
Hiodontidae		2	2	100
Ictaluridae	**ICTA**	**39**	**33**	**85**
Lepisosteidae		5	4	80
Moronidae		4	4	100
Mugilidae		1	0	0
Osmeridae		4	4	100
Percidae	**PERC**	**184**	**127**	**69**
Percopsidae		2	2	100
Petromyzontidae	**PETR**	**18**	**18**	**100**
Poeciliidae	**POEC**	**14**	**10**	**71**
Polyodontidae		1	1	100
Salmonidae	**SALM**	**36**	**34**	**94**
Syngnathidae		2	2	100
Umbridae		4	4	100

Species count indicates the number of species of each family included in original dataset of 777 species. Species count with greater than three traits shows the number of species in each family with at least four of the 7 life history traits. The far right column indicates the percent of species with 4 or more traits of the number of species originally included in the dataset. Bold font indicates the 11 families highlighted in the PCoA analysis by family code.

Life history trait diversity

We first evaluated the fish life history continuum model of Winemiller & Rose (1992) by plotting species' positions in relation to three life history

Table 2. Seven continuous life history traits with descriptions and summary statistics including mean, minimum (Min), maximum (Max), and standard deviation (SD).

Trait	Description	Mean	Min	Max	SD
MaxBodyL	Maximum total length (mm)	256.1	25.0	4030.0	378.0
LenMat	Mean length at maturation (mm)	128.6	16.0	2440.0	187.3
Longevi	Maximum potential longevity or lifespan (years)	7.9	1.0	154.0	10.7
AgeMat	Mean age at maturation (years)	2.5	0.1	22.5	2.3
Fecund	Total fecundity (number of eggs or offspring) per spawning season per female	36442.1	6.0	2280000.0	173122.7
EggSize	Mean diameter of mature, fully yolked ovarian oocytes (mm)	1.7	0.2	6.5	1.0
ParentalC	Degree of parental care based on placement of zygotes, parental protection, and nutritional contribution (see text for definition)	1.2	0.0	5.0	1.2

axes: ln(fecundity), ln(length at maturation), and ln(egg size +1) + ln(parental care +1). This analysis was performed for 372 native species with reported values for fecundity, length at maturation, egg size, and parental care. This sub-set of species was representative across families. We also summarised life history trait variation within and among species by conducting a principal coordinate analysis (PCoA) on the species-by-trait matrix. PCoA is a statistical methodology to explore and visualise similarities/dissimilarities in multivariate data by optimally representing the variability of a multidimensional data matrix in ordination space with reduced dimensionality (Legendre & Legendre 1998). A species similarity matrix of the seven continuous life history traits was constructed for the 603 native species with ≥4 traits. All traits except parental care were log-transformed to help achieve multivariate normality, and all major families were evenly represented (Table 1). Trait similarity was calculated according to Gower's similarity coefficient (Gower 1971). Gower's coefficient is a metric able to accommodate missing values, an important property for our analysis given the lack of scientific knowledge of all trait values for all species. Statistical significance of the principal coordinates (eigenvalues) and trait contributions (eigenvectors) were assessed using Monte Carlo randomisation (9,999 permutations).

We examined family differences in species life history trait composition by employing DISTLM: distance-based multivariate analysis for a linear model that can be performed on any symmetric distance matrix, and whose statistical significance is tested by permutation (McArdle & Anderson 2001). Distance-based multivariate linear regression addresses two major challenges of nonparametric multivariate analysis of ecological data: (i) partitioning the variability in the data according to a complex design or model, and (ii) the analysis is based on a multivariate distance measure (such as Gower's) that is reasonable for ecological data. Included in this analysis were only those families with 14 or more species (11 families in total; Table 1). DISTLM is capable of handling unbalanced designs making it an appropriate statistical approach for our study with family group sizes ranging from 14 to 250 species.

We tested for family group differences in multivariate trait variation using PERMDISP2, a permutational test for homogeneity of multivariate dispersions (Anderson 2006). This method is a multivariate analogue to the univariate Levene's test and is flexible because it can be based on any ecologically-relevant dissimilarity measure. This test computes an *F*-statistic to compare the average distance from an individual sample score (species) to the group (family) centroid defined by the principal coordinate (PC) space of a chosen dissimilarity measure (in our case, Gower's dissimilarity) and then permutes the appropriate least-squares residuals to estimate statistical significance. All data transformations and analyses were performed in R using the Vegan library (R Development Core Team 2008).

Geographic patterns in life history strategy composition

We assembled present-day occurrence data for native fishes in 350 watersheds of the United States and Canada according to the U.S. Geological Survey 4-digit catalog unit (NatureServe 2004) and Canadian watersheds compiled by N. E. Mandrak (Great Lakes Laboratory for Fisheries and Aquatic Sciences, Department of Fisheries and Oceans, Canada). Data sources included the scientific literature, U.S. state natural heritage programs, and questionnaires sent to biologists working at federal, state, and provincial agencies, universities, and museums. This dataset represents the most complete distributional information possible for these species at the level of sub-watershed in the U.S. and Canada. Occurrence data was unavailable for Alaska. Although watersheds of the Great Lakes were included, the Great Lakes proper were excluded from the geographic analysis.

The percentages of species assigned to each of the three life history strategies were mapped for North American watersheds. The process of assigning a species to a life history strategy can involve a hard classification into a single strategy or a soft classification according to a species' relative affinity toward each strategy (Olden & Kennard 2010). To illustrate large-scale geographic patterns of life history strategies, we chose to hard-assign each species to one of the three life history strategies by calculating the Euclidean distance in trivariate life history space between the species' position and the strategy endpoints and designating the species to the closest strategy. Strategy endpoints were defined as the following: opportunistic (minimum fecundity, minimum juvenile investment, and minimum maturation size), periodic (maximum fecundity, minimum juvenile investment, and maximum maturation size), and equilibrium (mean fecundity, maximum juvenile investment, and maximum maturation size). This calculation was based on normalised trait values (i.e., standardised range between 0 and 1 for each trait) to ensure equal contributions for the three life history parameters. A preliminary data analyses found a strong correlation between values based on hard and soft assignments for opportunists ($R = 0.932$, $P < 0.001$), periodic strategists ($R = 0.879$, $P < 0.001$), and equilibrium strategists ($R = 0.894$, $P < 0.001$); see also Olden & Kennard (2010).

Ternary plots were used to compare the life history composition of 8 major drainage basins to explore between- and within-basin geographic trends of dominant life history strategies. These basins included the Yukon, Western and Northern Hudson Bay, Pacific Northwest of the United States, Missouri, New England, Lower Colorado, Texas-Gulf coastal rivers, and South Atlantic-Gulf. These major drainages were selected because they represent disparate geographic regions with differing climates, geomorphology, hydrology and zoogeographic histories.

Results

Life history trait variation

We found strong conformity of North American freshwater fishes to the life history continuum model of Winemiller & Rose (1992), where opportunistic, periodic and equilibrium life history strategies are defined by trade-offs between generation time (length at maturation), fecundity and juvenile survivorship (investment per progeny) (Fig. 2a). The fish fauna was well defined by a triangular adaptive surface where a two-dimensional linear plane showed a strong statistical fit to the data (Fig. 2b, Pearson's $R = 0.85$, $n = 372$, $P < 0.0001$).

The trilateral life history model is also supported by the multivariate analysis of 603 freshwater fish species (Fig. 3). Ordination of fish species according to seven life history attributes revealed two major gradients of trait variation represented by the first two PCoA axes which explained 57.8% and 15.3% of variation, respectively (both statistically significant at $P < 0.001$ based on Monte Carlo randomisation). The first PC revealed a gradient from periodic strategists (i.e., relatively larger species with a long life span, later maturation, and high fecundity) associated with negative scores to opportunistic strategists (i.e., relatively smaller species with a short life span, earlier maturation, and low fecundity) with positive scores. The second PC distinguishes species exhibiting high parental care and large egg size with positive scores (i.e., equilibrium strategists), from species showing minimal parental care and smaller egg size with negative scores (Fig. 3a,b).

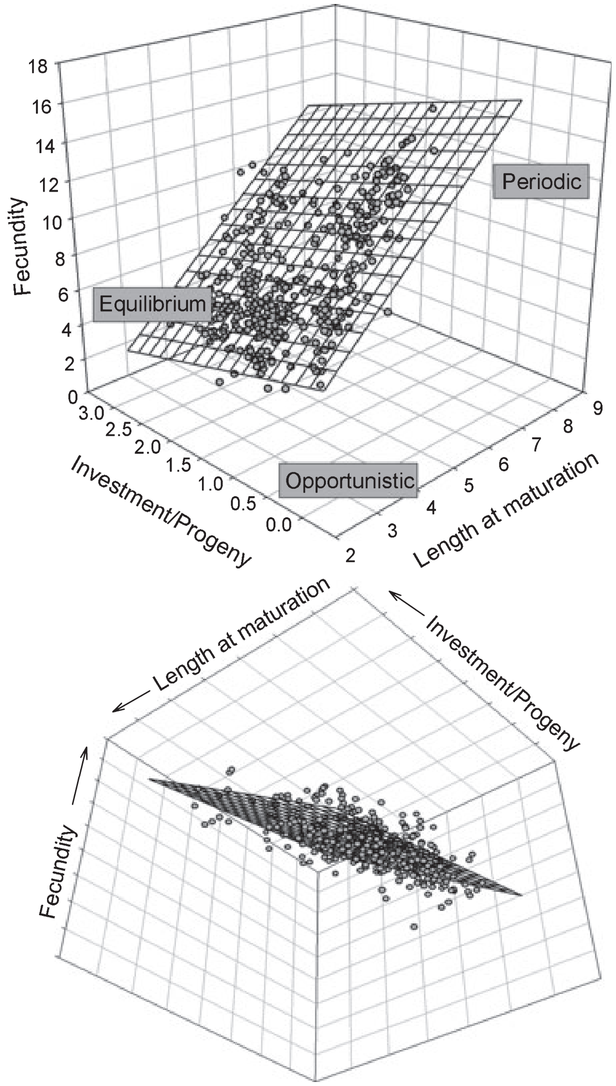


Fig. 2. Life history diversity of 372 freshwater fish species from the United States and Canada. (a) Species are located on a two-dimensional triangular surface, embedded in the three-dimensional space established by three axes: ln(fecundity), ln(length at maturation), and ln(egg size +1) + ln(parental care +1). The vertices of the surface define three endpoint strategies: opportunistic, periodic, and equilibrium; intermediate strategies are recognised within the gradient of life histories. (b) A three-dimensional linear plane fitted to all species (Pearson's $R = 0.85$, $n = 372$, $P < 0.0001$).

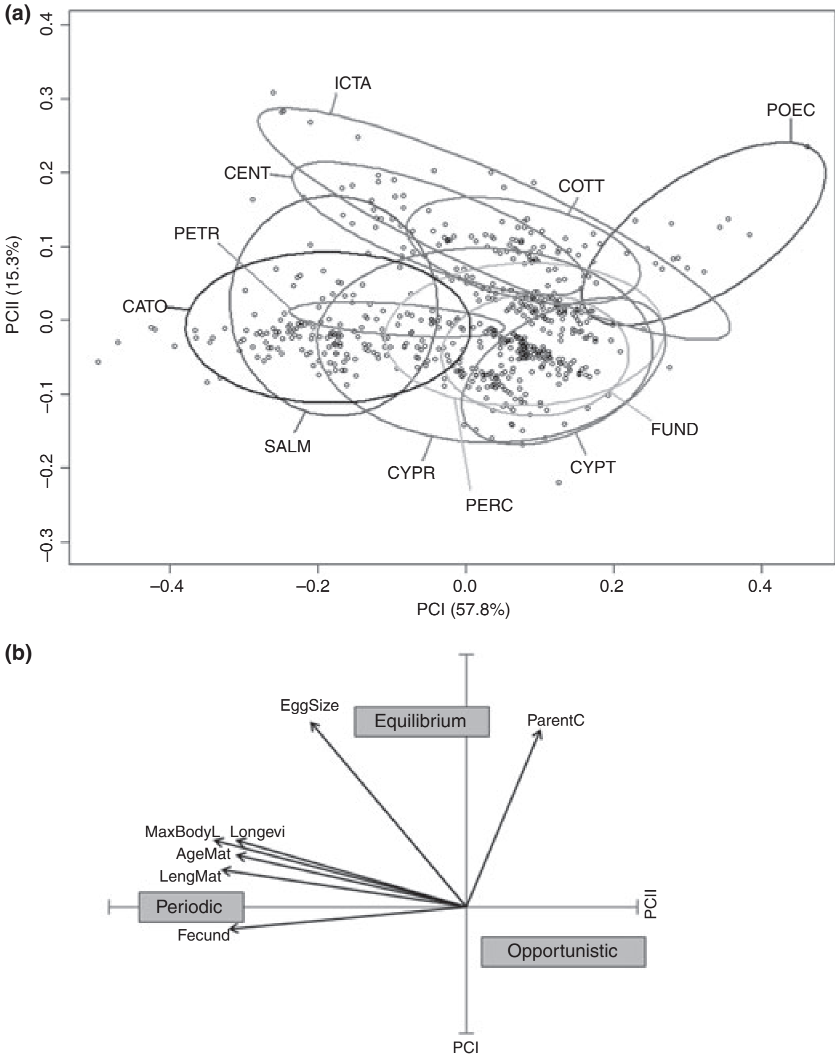


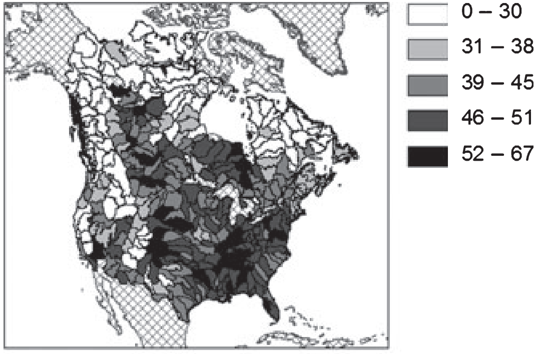
Fig. 3. Principal Coordinate Analysis (PCoA) of 603 freshwater fish species according to seven life history traits for (a) 11 major family groups (abbreviations from Table 1) within 95% confidence intervals. (b) Eigenvector plots of traits, and multivariate position of the three end-point strategies based on trait correlations.

Higher-level taxonomic patterns in life history trait variation are evident by examining the position of fish families in multivariate space (Fig. 3a). Ninety-five percent confidence ellipses for each family group show a wide range of variation between family groups with some families exhibiting low life history diversity and others spanning much of the trait ordination space. Differences in family trait composition are supported by the test of between-group dispersion, or group location in multivariate space, which revealed statistically significant separation in trait composition (DISTLM, $F = 4.55$ for centroids, $F = 3.75$ for spatial medians, $P < 0.001$). This result is expected considering the large differences between some family groups in multivariate space. For example, *Poeciliidae* exhibited the highest scores for PCI and relatively high scores for PC II (Fig. 3a) and is associated with higher parental care (Fig. 3b). By contrast, *Salmonidae* had some of the lowest scores along PC I and both positive and negative scores along PC II (Fig. 3a), which correlate with a suite of traits including high fecundity, high age at maturation, and a long life-span (longevity) (Fig. 3b). Other families exhibited limited separation in multivariate location (e.g., *Cyprinidae* and *Percidae*). Within-group dispersion varied among family groups as well (PERMDISP2, $F = 4.14$, $P < 0.001$). Species in the families *Cottidae*, *Fundulidae* and *Petromyzontidae* exhibited the least variation, whereas *Cyprinidae* and *Ictaluridae* displayed the highest diversity in trait composition.

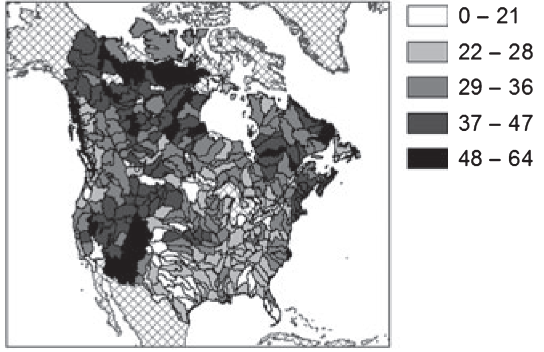
Geographic patterns in life history strategy composition

We found marked geographic patterns in the life history composition of watersheds across North America (Fig. 4). Latitudinal and longitudinal patterns across watersheds were discernable as were patterns associated with large topographic features such as coastlines and major mountain ranges, indicating that broad-scale zoogeographic processes have played a major role in shaping patterns of life history diversity. The opportunistic strategy was most prevalent in fish

(a) % opportunistic



(b)% periodic



(c)% equilibrium

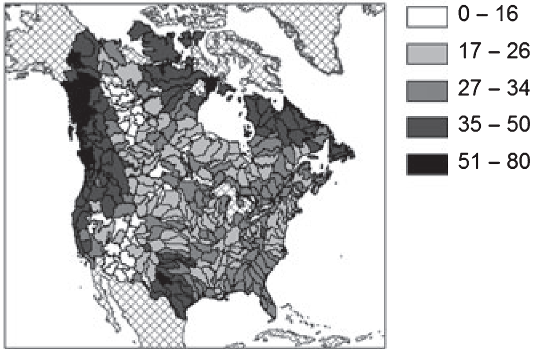


Fig. 4. Life history composition of freshwater fish species for 350 North American watersheds according to the percentage of species assigned to each life history: (a) opportunistic, (b) periodic, and (c) equilibrium. Shading has five levels that indicate 20th percentile increments of life history strategy representation for each panel. Species are hard assigned to a single life history strategy, and percent strategy representation in each watershed is calculated by species occurrence. Hatched area indicates watersheds not included in the analysis due to a combination of lack of trait data and lack of species occurrence data.

faunas throughout the southeast of the continent with *Cyprinidae* and *Percidae* families (the majority of which were classified as opportunists) dominating these watersheds. In addition, watersheds of the Lower Colorado River, Rio Grande, Arkansas, White and Red Rivers, Upper Mississippi and Missouri Rivers, tributaries of the Great Lakes, Saskatchewan River, Peace River and tributaries of southern Hudson Bay were characterised by greater percentages of opportunistic species (Figs 4a and 5a). The presence of species with the opportunistic strategy generally declined toward the north and west (with notable exceptions listed above) where watersheds were for the most part dominated by periodic and equilibrium species.

The dominance of periodic strategists varied from relatively low in the southeastern United States to high in more western and northern watersheds with the presence of *Catostomidae* and periodic representatives from other families (Fig. 4b). Watersheds illustrating the highest proportion of periodic strategists include the Upper and Lower Colorado River, Churchill, Thelon and La Grande Rivers of the Hudson Bay Basin, Atlantic coastal rivers in the New England region, and rivers draining the Beaufort (Sea) Basin, including the Yukon, Mackenzie and Great Slave Lake Watersheds (Figs 4b and 5a,b). Equilibrium strategists were the dominant life history strategy in watersheds of the Pacific coast (largely because many *Salmonidae* species which dominate these watersheds were classified as equilibrium strategists) as well as in northern latitudes, including rivers draining the Canadian Arctic Archipelago, and the Churchill and Koksoak Rivers flowing to the Labrador Sea of the Atlantic Ocean (Fig. 4c). The equilibrium strategy also dominated watersheds in the Texas Gulf (e.g., Neches, Trinity, Brazos, Colorado and Nueces rivers) primarily due to the presence of the families *Ictaluridae* and *Centrarchidae* (Fig. 5a). This strategy was notably absent from the Rocky Mountain region and in arid watersheds of the southwest. Although we highlighted basins above that are dominated by particular strategies, we also observed relatively even contributions from each strategy (e.g., select basins in the Pacific Northwest and New England region; Fig. 5b).

Discussion

In recent years, there has been growing interest in the functional traits – characteristics of an organism that are linked with its fitness or performance – of freshwater fishes. The study of species trait distributions can be used to understand complex phenomena, including why fish live where they do, how many taxa can coexist in a place, and how they will respond to environmental change (Winemiller 2005; Olden et al. 2010). The development and exploration of large trait databases such as the one reported in this study and the database recently presented by Frimpong & Angermeier (2009) are an important step forward in advancing trait-based approaches to fish ecology. Both the taxonomic (603 fish species across 138 genera and

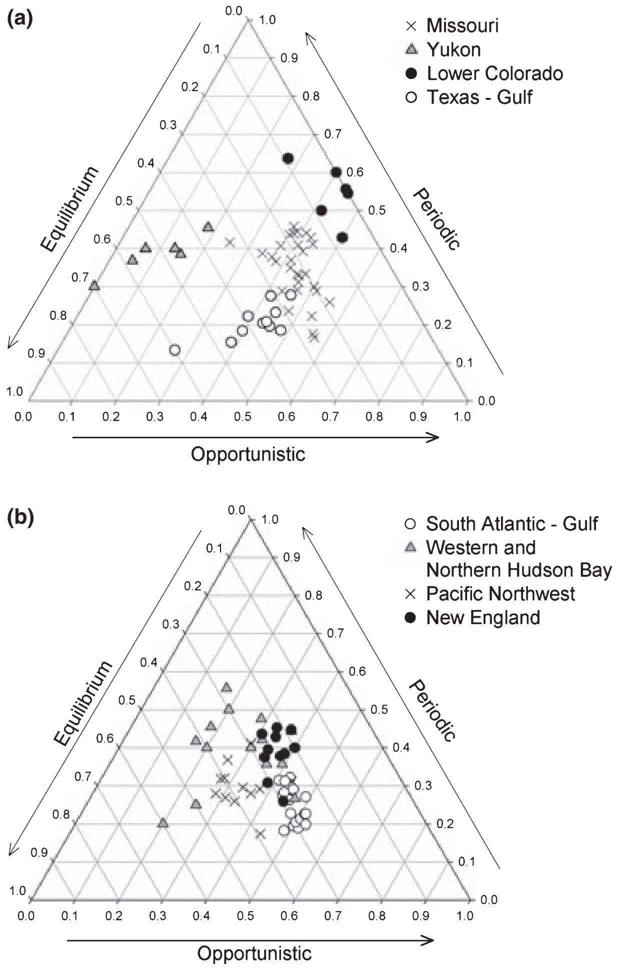


Fig. 5. Ternary plots illustrating for freshwater fish species the relative proportion of opportunistic, periodic, and equilibrium strategists in major drainage basins in the United States and Canada. Data points in ternary plots represent watersheds within major drainage basins (different symbols). Drainages are divided into two ternary plots (a and b) arbitrarily for easier viewing.

32 families) and geographic (350 watersheds across North America) scale examined in this study are unprecedented, insomuch that this study provides the first analysis of coupled taxonomic and geographic patterns of life-history trait variation of a continental fish fauna.

Major families of freshwater fishes exhibited both between- and within-family variation in functional composition as depicted in our multivariate trait analysis. A number of families exhibited a strong association with a particular strategy. These included killifish (*Cyprinodontidae*) and topminnows (*Fundulidae*) that were dominated by fish displaying the opportunistic strategy (early maturation, small-bodied, short-lived individuals), salmon and trout (*Salmonidae*) and suckers (*Catostomidae*) that were primarily associated with the periodic strategy (late maturing, large-bodied, long-lived, highly fecund individuals), and the catfishes (*Ictaluridae*) and sunfishes (*Centrarchidae*) that were mostly equilibrium strategists (high parental care, large egg size, medium body-size, and medium maturation age). Although numerous families were associated with a single dominant life history strategy, others had more variation in their composition. Included in these was *Cyprinidae*, the largest family of freshwater fishes, which encompass species considered to be opportunistic (e.g., chubs, daces, shiners), periodic (e.g., pikeminnows) and intermediate between periodic and equilibrium (e.g., carp). Other diverse families included *Percidae* containing darters (opportunistic and periodic) and perches (equilibrium) and *Ictaluridae* containing madtoms (opportunistic) and bullheads and catfishes (equilibrium). Overall, our analysis revealed that family-level associations with life history strategies both exist and are variable among freshwater fishes of North America.

In agreement with previous studies we found significant support for the three-strategy life history continuum model of Winemiller & Rose (1992), where opportunistic, periodic and equilibrium life history strategies are defined by trade-offs between generation time, fecundity and juvenile survivorship (Winemiller 1989; Vila-Gispert & Moreno-Amich 2002; Vila-Gispert et al. 2002; King & McFarlane 2003; Erös 2005; Olden et al. 2006). An important consideration for the life history model of Winemiller & Rose (1992) is that trait variation (and hence trade-offs among these traits) is continuous – therefore strategies intermediate of the three end-points are expected. We found support for the continuous nature of trade-offs between the three end-point strategies, rather than large clusters of species near the end-point strategies. Consequently, we highlight the fact that species life history strategies can be assigned in one of two ways. According to a ‘soft’ assignment, each species can be characterised by its degree (percentage) of similarity to each strategy, for example by calculating a species multivariate trait distance to each end-point strategy. Alternatively, a ‘hard’ assignment involves allocating each species into a single life history strategy according to the minimum multivariate trait distance to each end-point strategy. Soft life history assignments are advantageous because they provide a more realistic depiction of most species that fall intermediately between two or three strategies and thus cannot be easily assigned to a single strategy (see Fig. 2). However, when examining life history trends across basins, we found a strong correlation between values based on hard and soft assignments (see also Olden & Kennard 2010). To illustrate large-scale geographic patterns of life history strategies, we chose to use hard assignments to generate three distinct groups (see Fig. 4).

We found that life history strategies of freshwater fishes exhibit geographic patterns consistent with regional climatic regimes (i.e., latitudinal gradients) and past historical events in North America. In general, we observed a latitudinal gradient of smaller-bodied, short-lived species (generally opportunistic strategists) at low latitudes to large-bodied, longer-lived species (generally periodic equilibrium strategists) at high latitudes. This is in agreement with previous studies that found similar correlations between increasing latitude and larger-bodied species with a longer time to maturity (Vila-Gispert et al. 2002; Blank & Lamouroux 2007).

Selective pressures of historical processes both influence and bound the limits of present-day species diversity, and it is thus important to consider the trends we observe in light of past selective events (Jackson & Harvey 1989; Mandrak 1995; Magnuson et al. 1998; Jackson et al. 2001). The geographic trends in life-history variation observed in this study are explained at least in part by selective extinctions during the Pleistocene glaciations (Moyle & Herbold 1987; Mahon 1984; Irz et al. 2007). Freshwater fishes in northern drainages (present-day Canada and the northern-most portion of the United States) and further south along the Rocky Mountains were either forced to migrate or faced extinction from glaciation events during the Pleistocene (Smith 1981). Along the West Coast, glaciation selected for periodic strategists capable of migrating large distances to more suitable environments and able to persist through conditions unsuitable for successful reproduction (e.g., long-lived species) (Moyle & Herbold 1987). Our results are congruent with this theory as we found that the western drainages were dominated by equilibrium strategists along the coast and by periodic strategists further inland along the Rocky Mountains. The Mississippi and Missouri drainages as well as river basins at lower latitudes, particularly along the east coast, remained largely unglaciated during the Pleistocene. However, freshwater fishes in these drainages were subjected to extreme conditions including habitat desiccation and variable hydrologic regimes that resulted in repeated episodes of habitat isolation, fish recolonisation and community assembly. The species with opportunistic life histories were better able to capitalise on these conditions and exhibit long-term persistence in these environments (Mahon 1984; Moyle & Herbold 1987). Our geographic investigation of life history variation supports this theory as we found that the prevalence of the opportunistic life history was generally highest in the southeastern portion of the continent. It is also worth noting the dominance of the opportunistic strategy in basins of the desert southwest where small-bodied species capable of rapid colonisation are typical (Fig. 4a) (Olden et al. 2006).

Although trait-based approaches have witnessed greater attention in recent years, their application is not without limitations. It is possible that some trade-offs may not be detectable with the given suite of adult traits studied, especially because traits of some species, particularly trophic or behavioural traits, can differ throughout the lifecycle (McCann 1998). Although trait-based approaches (and their associated statistical analysis) rarely account for within-species variation, fuzzy coding can be used to record biological traits, which allows for variation within a taxon for a specific trait (Chevenet et al. 1994). However, when examining life history traits such as those included in this study, previous studies suggest that between-species variation generally exceeds within-species variation (Blank & Lamouroux 2007). Another limitation is that hard-assigning species to life history strategies requires that species with intermediate strategies be forced into one strategy (see previous discussion). For example, in our geographic analysis, the composition of Pacific coastal rivers was shown to be predominantly equilibrium, in large part because of the prevalence of salmonids that are classified as equilibrium strategists using a hard-assignment rule. However, in reality most salmonids exhibit a life history intermediate between equilibrium (large egg size and high parental care) and periodic (large body size and late maturation).

The use of trait-based approaches to address ecological problems is increasing (Petchey & Gaston 2006; Webb et al., in press), and thus it is imperative that large databases such as the life history trait data base described here are explored for utility as well as limitations. This study described life history trait variation of freshwater fishes of Canada and the United States and found three major patterns. First, multivariate trait analysis supported the life history continuum model of Winemiller & Rose (1992) by identifying the three end-point strategies of equilibrium, opportunistic and periodic. Second, families of fishes differed both in their composition of strategies and in the degree of within-family variation. Third, watershed-scale patterns of life history variation were discernable and were congruent with biogeographic processes shaping the occurrence of life history strategies of freshwater fishes throughout North America. In combination with similar trait investigations for other freshwater taxa, including macrophytes (Bornette et al. 1994), aquatic insects (Poff et al. 2006; Verberk et al. 2008; Statzner & Bêche 2010), crayfish (Larson & Olden, in press) and amphibians (Sodhi et al. 2008), we believe that freshwater ecologists are well posed to advance trait-based approaches in their studies.

Acknowledgements

We thank two anonymous referees for their comments that improved the final manuscript, and Nick Mandrak for graciously providing fish distribution data for Canada. We also thank David Lawrence for his help with obtaining and organising fish distribution data for the United States. Funding support was provided by a Cobb Fisheries scholarship and University of Washington Top Scholar scholarship (MCM) and the USGS Lower Colorado River Basin Aquatic GAP Program (JDO). MCM and JDO conceived and developed the idea for the manuscript. JDO and ZRS assembled the trait database, MCM conducted the data analysis, and all authors wrote the manuscript.

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